

Luminance Transduction and Contrast Discrimination Measured by Afterimages

THESIS

presented to the Faculty of Arts
of
the University of Zurich
for the degree of Doctor of Philosophy

by

FRIEDRICH HEITGER
of Koblenz (FRG)

Accepted on the Recommendation of Professor Norbert Bischof Ph.D.



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Chapter I

INTRODUCTION

The fact that the light in a visual scene can vary by dramatic amounts, represents a serious problem for a sensory device such as the eye. The human visual system, however, seems to have solved this problem quite elegantly. With a dynamic range of more than ten decades, it is able to function under conditions ranging from the the brightest daylight to the dimmest moonlight. In addition, and perhaps more importantly, it can discriminate even minute differences in intensity within this range.

The question of how physical light intensity is transduced into a physiological representation has interested psychophysicists and neurophysiologists for a long time. The early investigations were not so much concerned with the underlying physiological mechanisms as with discerning the relationship between the physical stimulus and its perceptual correlate. Fechner, in the 19th century, was the first to propose a relation between the two based on a mathematical deduction from Weber's law. Weber found that the just noticeable difference (jnd) between two stimuli was linearly proportional to the stimulus intensity. This implied that the jnd divided by the intensity of the stimulus remained constant. Assuming that the jnd was also a constant quantity in the sensory domain, Fechner deduced that a geometrical progression of intensity in the physical domain would result in a linear progression in the perceptual domain. This assumption known as Fechner's law was very popular in the 19th century, but began to be seriously criticised at the beginning of the 20th century (Parsons, 1915).

With the empirical findings of Stevens (1957), Fechner's logarithmic law was finally abandoned. Using magnitude and ratio estimation as a method of

determining the subjective strength of a stimulus, Stevens found that a power law provided a better description for a number of sensory continua (The problems arising with the method itself (Poulton, 1968), and with its applicability to the sensory transducer stage (MacKay, 1963) will be discussed below).

More recent evidence, however, indicates that the transducer characteristics of retinal receptors, if recorded over a sufficient range of stimulus intensity, fit neither Fechner's logarithmic function nor Stevens' power function (Zwislocki, 1973, 1974). Instead, the transducer functions of the receptors appear to be S-shaped, with a lower segment of increasing slope and a saturating upper end (e.g. Naka and Rushton, 1966). Many psychophysical investigations support such a function (e.g. Hood et al., 1978; Maudarbo-cus, 1973; Virsu and Laurinen, 1977), but others still support power functions (e.g. Mansfield, 1976), or even accelerating functions (Nachmias and Rogowitz, 1983). Thus the issue has not yet been decided. Present discussions, however, seem to be less concerned with the particular shape of the transducer function as with the problem of how the function changes with different levels of ambient illumination (adaptation).

In the present investigation the problem of luminance transduction was looked at with an entirely new method, based on an afterimage effect generated with plaid patterns. The method provided a means not only of investigating the transduction properties of the visual system, but also of measuring its sensitivity to contrast for different pattern luminances and contrasts.

Chapter II

METHODS

2.1 The Afterimage Effect

If one shifts the gaze back and forth between the two points indicated in the center region of the plaid pattern depicted in *Fig.1a*, a diagonal afterimage grid, similar to the pattern shown in *Fig.1b*, will appear immediately after the offset of the stimulus and will last for 1-3 seconds.

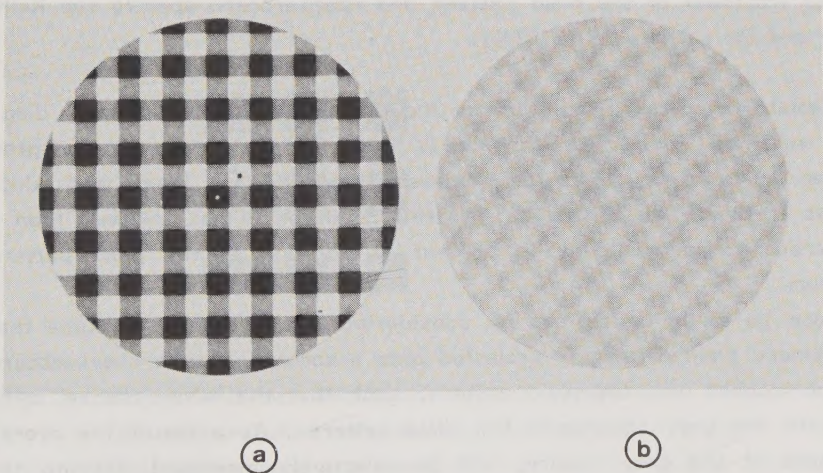


Fig. 1: The afterimage effect.

(a) plaid pattern and fixation points

(b) diagonal afterimage grid

The afterimage grating resembles strongly the diagonally oriented fundamental Fourier components of a checkerboard, having a check-width identical to the 'bar' width of the plaid pattern.

2.1.1 Fourier Spectra of Plaid and Checkerboard Patterns

The existence of such a diagonal afterimage grid is surprising, because a plaid pattern does not contain any of the spatial Fourier components present in a checkerboard. This is demonstrated in *Fig.2*, where the two-dimensional Fourier spectra of the plaid and the checkerboard are depicted next to the pattern. The plaid pattern spectrum (*Fig.2a*), which can be regarded as the linear superposition of two orthogonal square-wave gratings, shows only power in the horizontal and vertical orientations. Compared to this the checkerboard spectrum (*Fig.2b*) looks entirely different: The main power (fundamental components) is located in the diagonal orientations, and the other components (higher harmonics) are distributed over almost all orientations, except the vertical and horizontal (for a more detailed treatment of the plaid pattern and checkerboard spectra see Kelly (1976) and De Valois et al. (1979)).

An absolutely necessary condition for the plaid pattern not containing diagonally oriented Fourier components is that the luminance of the grey squares must be equal to the arithmetic mean of the black and white squares (ordinary plaid pattern). If this condition is not fulfilled, then a checkerboard spectrum will be present in addition to the plaid pattern spectrum.

This can be easily understood by considering the following: Imagine that an ordinary plaid pattern is projected onto a screen. Then a checkerboard is superimposed onto the plaid pattern, such that the 'white checks' coincide with the grey squares of the plaid pattern. As a result the overall luminance of the grey squares will be selectively increased, leaving the luminance of the black and white squares unchanged. Any deviation of the luminance of the grey squares from the arithmetic mean of the black and white squares can be thought of in terms of the additional presence of a checkerboard; be it additive, as in the example above, or subtractive. The overall Fourier spectrum of such an 'unbalanced' plaid pattern will therefore

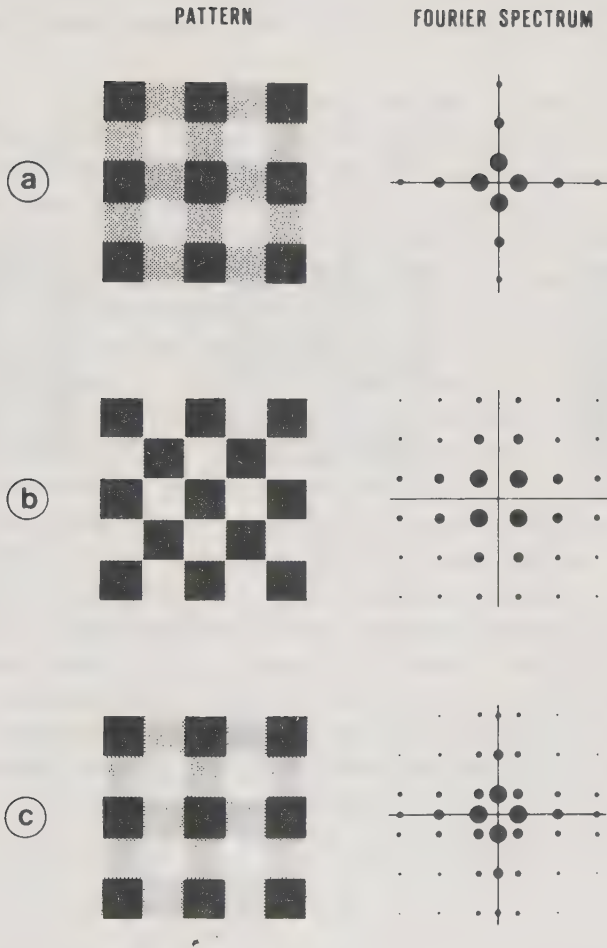


Fig. 2: Pattern and two-dimensional Fourier spectrum.

(a) ordinary plaid pattern and spectrum.

(b) checkerboard and spectrum.

(c) 'unbalanced' plaid pattern and spectrum.

In the spectral plots, the Fourier components are represented in terms of their relative magnitude (size of circles), spatial frequency (distance of circles from origin) and orientation (angular position of circles)

contain a checkerboard spectrum superimposed on the spectrum given by the two orthogonal square-wave gratings. This is demonstrated in *Fig.2c*.

Another, simpler, way of demonstrating the existence of two-dimensional Fourier components is given by the method of length integration: When an oriented line operator, integrating all intensity values underneath it, is shifted across a pattern, the modulation of its output will indicate the presence of the Fourier components specific to its orientation. For example, if the operator is shifted in an diagonal orientation across the plaid pattern, the output will be flat, as shown in *Fig.3a* (because the plaid pattern is periodic, the operators length must not be infinite, but can be restricted to the diagonal extent of two plaid pattern elements). However, a selective increase (*Fig.3b*) or decrease (*Fig.3c*) of the grey squares' luminance introduces a triangular modulation of the operators output. A shift of 180° in relative phase can be observed by comparing the two conditions. If the line integrator is shifted across a checkerboard pattern, the output will be very similar to that obtained with plaid patterns of the kind depicted in *Fig.3b* and *3c*. Thus, the line integration method also demonstrates clearly the existence of diagonally oriented Fourier components for the case when the luminance of the grey squares is not equal to the arithmetic mean of the black and white squares in the plaid pattern (For a complete Fourier description, the triangular-wave has to be further decomposed into its one-dimensional sine-wave components. Since this aspect is of no importance for the present argument, it will not be treated here).

2.1.2 The Paradox

The above considerations provide a means of explaining the presence of diagonal spectral components in the plaid pattern. However, they fail to explain a seeming paradox: It is the ordinary plaid pattern, with no diagonal Fourier components, which generates the strong diagonal afterimage grid.

There are two possible ways to resolve this paradox. First, it may be argued that the spectral properties of the plaid pattern have nothing to do with the afterimage effect, which implies that a Fourier description of the stimulus is inappropriate. Second, it may be argued that the physical spec-

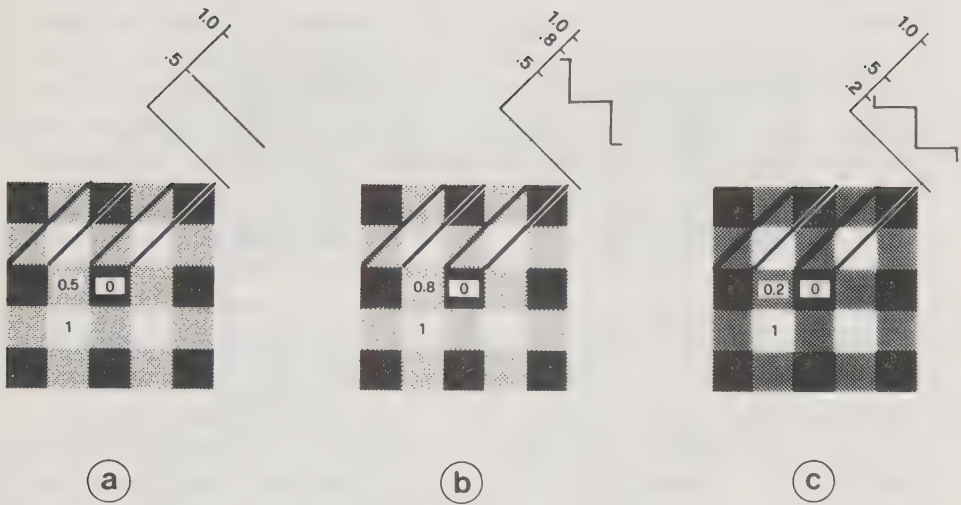


Fig. 3: The line operator method.

The absence (a) or presence (b and c) of diagonal Fourier components can be demonstrated with a line operator that integrates intensity values along its length. The inset values represent the respective intensities of the plaid pattern elements.

tral properties of the ordinary plaid pattern are considerably altered by the visual system's non-linear transduction of luminances. A compressive transduction of luminance, for example, would cause a distortion of the relative luminances in the ordinary plaid pattern, such that the brightness of the grey squares would not be equal to the arithmetic mean of the black and white squares. Thus, even if, in the physical domain, there is no checkerboard spectrum present in the ordinary plaid pattern, it may exist after transduction.

In *Fig.4* this is demonstrated once again with the method of the line operator, introduced above. This time the response values (see inset values) are integrated according to the transducer functions located below the pattern. In the case of the linear transducer function depicted in *Fig.4a*, the output of the line operator, shifted diagonally across the plaid pattern, will be flat. On the other hand, if there is a compressive transduction (e.g. logarithmic), the output of the integrator will be modulated, indicating the presence of the diagonally oriented Fourier components of a checkerboard (*Fig.4b*).

There is a straightforward way of testing this transduction hypothesis. If the checkerboard spectrum, introduced by non-linear transduction, is responsible for the diagonal afterimage grid, then the afterimage should disappear when the luminance of the grey squares is set to a value, which corresponds to the mean of the black and white squares after transduction. In other words, lowering the luminance of the grey squares to a value which will give a response of 5.9 in *Fig.4b*, should make the output of the line integrator flat again. By lowering the luminance of the grey squares further, the modulation will reappear, but then with an inverted phase.

2.1.3 An Experimental Test

During an experimental test of the transduction hypothesis, a range of luminances for the grey squares was indeed found, for which the adaptation to the plaid pattern was not followed by an afterimage. Furthermore, in accord with the hypothesis, an increase or decrease of the grey squares' luminance beyond this range, caused a return of the diagonal afterimage grid.

As was expected, the relative phase of the afterimage grid also changed its sign in the two conditions: The upper limit, where the afterimage reappeared, was followed by an afterimage grid with dark diagonal 'stripes' running through the positions previously occupied by the grey squares of the plaid pattern. The reverse held true for the lower limit, where bright 'stripes' appeared in these positions. Thus, the afterimage grid was always 180° out of phase with respect to the checkerboard fundamental components. It therefore can be regarded as a negative afterimage. *Fig.5* illustrates the two afterimage and the 'no-afterimage' conditions.

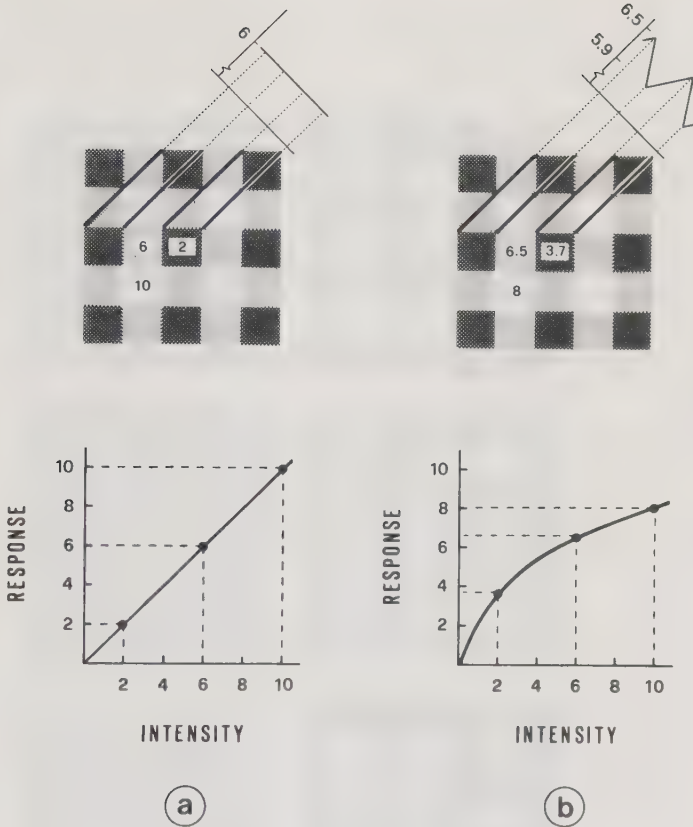


Fig. 4: The non-linear transduction hypothesis.

(a) Linear transduction:

For an ordinary plaid pattern the integration of the transduced intensity values (insets) results in no diagonal Fourier components being present.

(b) Compressive transduction:

For the same pattern a compressive transduction introduces the presence of diagonal Fourier components.

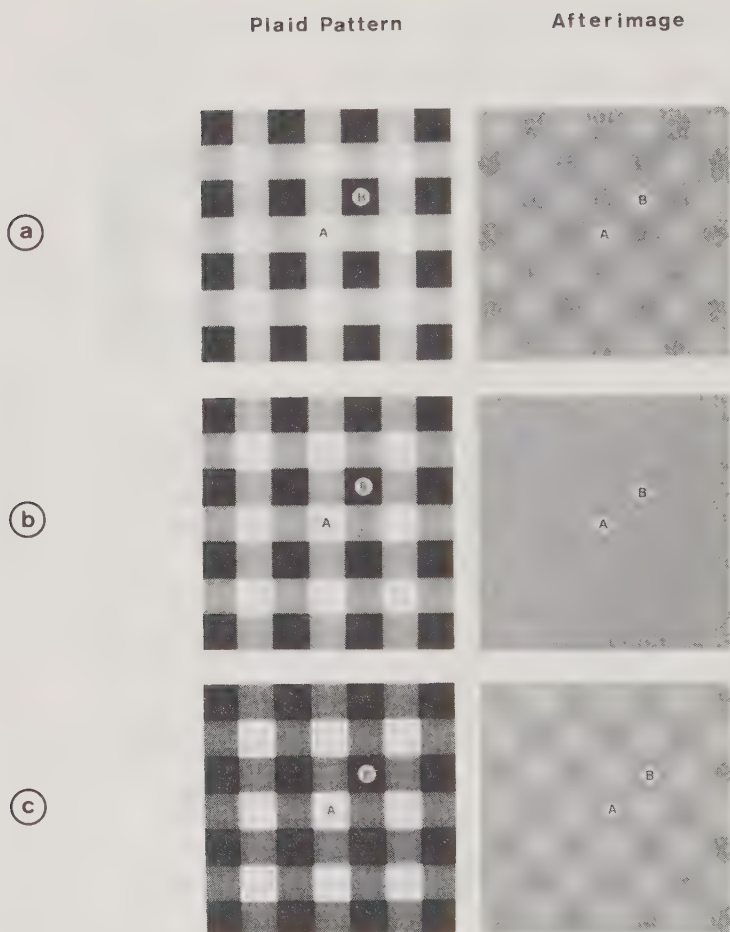


Fig. 5: The afterimage experiment.

(a) upper threshold for the presence of an afterimage following adaptation in points A and B

(b) no afterimage following adaptation in points A and B

(c) lower threshold for the presence of an afterimage following adaptation in points A and B

2.1.4 Interference and Afterimages

There is an important aspect concerning the generation of the afterimage grid that has not been mentioned yet. In the two fixation points indicated in *Fig. 1a*, the two component square-wave gratings of the plaid pattern are 180° out of phase. This counterphase relation also applies to the Fourier components of the square-wave gratings, which constitute the plaid pattern. It does not, however, apply to the Fourier components of the checkerboard, which have identical phase with respect to the two fixation points.

In previous studies, where a similar adaptation technique was used to generate afterimages of the fundamental and third harmonic Fourier components of the checkerboard (Heitger, 1982), the following rule for afterimage generation was established: The Fourier components in phase at the two fixation points will appear as a negative afterimage, whereas those in counterphase will cancel and will not be present in the afterimage. This rule, therefore, allows the theorem of interference to be applied to the prediction of afterimages of Fourier components.

The adaptation technique applied to the plaid pattern will result in all the horizontally and vertically oriented Fourier components of the plaid pattern (square-wave components) being adapted in a peak subtract mode and all the checkerboard components being adapted in a peak add mode. Thus, when there are checkerboard components present in the plaid pattern, the adaptation technique will selectively filter them out and they will consequently be seen as an afterimage.

2.2 General Procedure and Experimental Parameters

The upper and lower threshold values for the luminance of the grey squares for which no afterimage occurs following adaptation, can be considered as the limiting conditions for the processing of the checkerboard fundamental Fourier components. The mean of these values will then represent the luminance value for the grey squares that is located midway between those of the black and white squares of the plaid pattern. This value

necessarily depends on the transducer function of the visual system. In case of a linear function, for example, it should correspond to the arithmetic mean of the black and white squares, whereas for a logarithmic transducer function it should correspond to the geometric mean.

Thresholds for the appearance of the afterimage were determined by the method of ascending limits for eight pattern contrasts ranging from 0.1 to 0.8 and ten pattern-average luminances between 0.022 and 22 cd/m². Pattern contrast was defined as the Michelson contrast between the black and white squares $((L_{\max} - L_{\min}) / (L_{\max} + L_{\min}))$ and pattern-average luminance as the arithmetic space-averaged luminance of the plaid pattern.

Three subjects, including the author, all of whom had normal or corrected vision took part in the experiments. Two of the subjects were naive concerning the purpose of the experiment. Each subject adapted to the plaid pattern by shifting his gaze five times back and forth between two fixation points. These points were located in the center of a white and a black square element of the plaid pattern (see *Fig. 1a*). Two small LED's, which were sequentially illuminated, served as an aid to fixation. A short accoustical signal indicated the change of the fixation point every 800ms. This time interval was found to ensure careful fixation without the occurrence of additional saccades. At the end of the adaptation sequence the plaid pattern was replaced by a dim neutral background field. The subject then had to indicate if he had seen a diagonal afterimage grid or not, by pressing one of two buttons. The luminance of the grey squares was then altered and a new adaptation sequence started after a pause of 40 seconds.

The thresholds were always determined by starting with a luminance of the grey squares that resulted in no afterimage following the adaptation. The luminance of the grey squares was then incremented (upper threshold) or decremented (lower threshold), until an afterimage was detected. The amount of the increment or decrement depended on the pattern contrast, being 1% at low contrasts and up to 3% at high contrasts. Following the detection of an afterimage, the luminance of the grey squares was increased or decreased by 5-20%, depending on the condition. The exact amount depended on the pattern contrast and was randomized to avoid sequential viewing artifacts. Normally the subjects needed about two to six adaptation sequences to reach threshold again.

In the first experiments the upper and lower thresholds for a specific pattern condition were determined ten times. In subsequent experiments this number was reduced to three for the following reasons: One of the striking properties of the afterimage effect is that the transition from the no-afterimage to the afterimage condition is very sharp. In fact, a variation of only about 1 to 3% in the absolute luminance of the grey squares is sufficient to generate an afterimage grid. In most cases the scatter of the threshold points was on the order of reliability of the experimental apparatus (about 0.5%). (Usually the standard deviations for the threshold points lay within 0.5% to 2% of the grey square's absolute luminance.)

Since the thresholds could be reliably reproduced at the level of calibration errors, a relatively small number of threshold samples was deemed sufficient. In the rare cases where a large scatter in the threshold values occurred, the sampling was continued until an acceptable standard deviation was obtained.

As already mentioned above, the upper and lower afterimage thresholds were determined for ten different pattern-average luminances (0.022, 0.055, 0.11, 0.22, 0.55, 1.1, 2.2, 5.5, 11 and 22 cd/m^2). Within a single session only the pattern-average luminance parameter was varied, whereas the pattern contrast was only changed between sessions (0.1 to 0.8, in increments of 0.1). Upper and lower thresholds for the appearance of the afterimage were, therefore, determined for 80 different plaid patterns.

The spatial frequency of the component square-wave gratings was 0.9 c/deg, giving a spatial frequency for the checkerboard fundamental Fourier components of 1.3 c/deg. Other investigators (Corwin et al., 1976) have found that the visual system is most sensitive to afterimage gratings at this spatial frequency. The pattern was circular and extended over 11° of visual angle. The viewing distance was 2.2 meters.

2.3 Apparatus

2.3.1 Projection Methods

The plaid pattern was generated by three modified slide projectors (Leitz, Pradovit, 250 Watts) equipped with tungsten iodine lamps. One of the projectors provided a grid pattern (depicted in *Fig.6a*); a second a checkerboard pattern (*Fig.6b*); and a third a uniform background field. Using a half-silvered mirror, the images of the two 'pattern' projectors were superimposed in the way shown in *Fig.6c*.

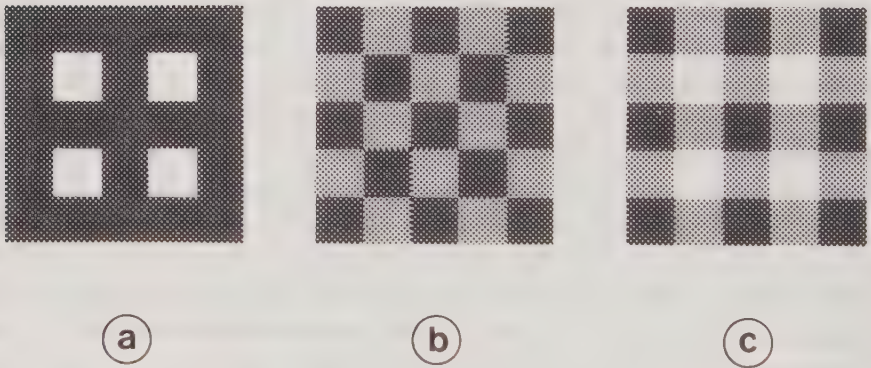


Fig. 6: The method of generating the plaid pattern.

The superposition of a projected grid (a) and a checkerboard (b) results in the plaid pattern (c).

The intensity of all three projectors could be independently adjusted by means of servo-controlled polarizers and neutral density filters. By combining the images of the two 'pattern' projectors, a plaid pattern could be

generated in which the luminance of the white squares was controlled by the 'grid' and the luminance of the grey squares by the 'checkerboard' projector (*Fig.6c*). The luminance of the black squares could be varied by the third projector. Because the third projector produced a uniform field, it also contributed to the luminance of the grey and white squares in the plaid pattern. Nevertheless, as the luminance needed for the grey and white squares was always higher than that needed for the black squares, the luminance of the former could be set by just adding the light of the 'pattern' projectors to the background field.

The calculation for the luminances of the black (b) and white (w) squares, with a fixed pattern contrast (C) and pattern-average luminance (L), is given by the equations below. The luminance of the grey squares (g), the experimental parameter, is expressed in terms of the percent deviation (p) from the geometric mean of the black and white squares.

Given

$$g = \sqrt{b \cdot w} + \sqrt{b \cdot w} \cdot p/100$$

and that

$$C = (w - b)/(w + b)$$

$$L = (w + b + 2g) / 4$$

are constant, then

(1)

$$w = \frac{2L \cdot (1 + C)}{\sqrt{1 - C^2} (1 + p/100) + 1}$$

$$b = \frac{2L \cdot (1 - C)}{\sqrt{1 - C^2} (1 + p/100) + 1}$$

The projectors were installed in a rack, directly behind and above the observer's heads. The inhomogeneities of the field produced by the projectors could be considerably improved by carefully aligning the condensor systems and the tungsten bulbs, as well as by rendering the glass cylinders opaque by finely grinding them. The remaining inhomogeneities did not exceed 2% over the area covered by the pattern.

2.3.2 Light Measurement and Sensors

The screen on which the pattern was projected consisted of highly diffusing photographic paper, mounted on a 0.5 by 0.5 meter frame. Two fixation LED's were attached to the back of the screen, such that their light could be seen by the observer through a small pinhole. The light falling onto the screen was measured directly by three photodiode sensors with integrated operational amplifiers (Moririca, MHA-200). The sensors were located at the lower part of the projected plaid pattern, such that they could sample the illumination (lux) at the positions of a black, a white and a grey square. The spectral sensitivity of the sensors was very close to that of the C.I.E. standard photopic observer. All the sensors were carefully linearized down to 0.01 lux by several independent procedures.

In order to convert the illumination values to measures of luminance, the sensors were calibrated with a Minolta and a UDT luminance meter. The conversion factor from lux to cd/m^2 was found to be 0.27. For a perfect white diffuser the conversion factor is $1/\pi$ (0.318): hence the reflectance of the screen was determined to be 85%.

As some of the experiments have been conducted under long-wavelength conditions, by using RG-630 (Schott) filters, the sensors have also been calibrated for this condition according to the C.I.E. photopic standard observer. The output of the sensors was temperature corrected using a formula given by the manufacturer.

2.4 Control over the Experiment

2.4.1 Hardware

The experiment was entirely controlled by a PDP-11/34 computer. A parallel interface (DR11-K) with a 16-bit input/output register served as a communication port for peripheral devices. The voltage output of the sensors was digitized by a 12-bit A/D-converter. The remaining input bits were used for the two decision buttons and for interrupt switches which allowed the the experiment to be returned to manual control.

The output port was used to control the following devices:

- electromagnetic shutters placed in front of the projectors
- servo-motors attached to the polarizers
- multiplexers controlling the output of the sensors
- fixation LED's
- buzzers for accoustical signals.

The desired luminance values for the black, white and grey squares in the plaid pattern were regulated via a software feedback loop, using the sensors to measure the luminance and the polarizers to change it. A second, temperature corrected, photodiode feedback circuitry kept the intensity of the light bulbs in the projectors extremely constant. Nevertheless, even small drifts in intensity were monitored by comparing the luminance values of the plaid pattern before and after the adaptation sequence. If the difference exceeded a certain limit, the data were discarded and the adaptation sequence was repeated.

2.4.2 Experimental Software

The software for the experiment was designed to automate the experimental procedure as far as possible. It controlled the sensors, polarizer servos, shutters, fixation LED's, buzzers, response buttons, software interrupt switches and the experimental timing. The experimental parameters, such as pattern contrast, pattern average luminance and the starting and

incremental/decremental luminances for the grey squares were submitted to the program as free variables before the experiment started. The upper and lower threshold conditions for the presence of the diagonal afterimage grid were stored in terms of the luminance of the black, white and grey squares at these points.

2.5 Mathematical Treatment of Data

2.5.1 Deviation from a Logarithmic Transduction

As already mentioned above, the purpose of the experiment was to find the range of luminances for the grey squares, in which no diagonal afterimage grid followed the adaptation to the plaid pattern. This can be considered as being equivalent to the condition where, for the visual system, the brightness of the grey squares is just midway between the black and white squares. If the transduction of luminance were logarithmic, one would expect to find upper and lower threshold values for the grey squares located around the geometric mean of the black and white squares. It turned out, that this was indeed the case for most of the experimental data. For this reason the threshold values for the grey squares were expressed in terms of the *percent deviation* from the geometric mean of the black and white squares. The geometric mean of the upper and lower threshold luminances of the grey squares thus corresponds to the 'physiological' mean luminance of the black and white squares. This mean value was calculated and also converted to percent deviation. Such a representation of the data is a very sensitive way to show how well the visual system performs compared to a perfect logarithmic transducer.

2.5.2 A Measure of Contrast Sensitivity

The difference between the upper and lower threshold values for the appearance of the afterimage grid can be regarded as a measure of how sensitive the visual system responds to the diagonal Fourier components,

that are contained in the plaid pattern. If, for example, the difference in the luminance of the grey squares for the upper and lower threshold condition is relatively large, the sensitivity may be considered as low and vice versa. However, the absolute luminance difference for the two threshold conditions is not a good representation of sensitivity because it depends on the pattern's average luminance. A better measure of sensitivity, which is independent of pattern-average luminance, is the *contrast threshold* for the diagonal Fourier components (checkerboard) resulting in an afterimage. This threshold contrast can be calculated according to the following assumptions:

The geometric mean ($m\%$) of the upper and lower threshold values ($u\%$, $l\%$) can be considered to represent the condition, where there (physiologically) are no diagonal Fourier components present. By taking $m\%$ as a reference value, $u\%$ and $l\%$ can be made symmetrical around $m\%=0$, by the following transformation:

$$u\%' = ((u\%+100)/(m\%+100)-1) \cdot 100 \quad (2a)$$

$$l\%' = ((l\%+100)/(m\%+100)-1) \cdot 100 \quad (2b)$$

The Michelson contrast of the diagonal Fourier components, necessary to reach threshold will then be

$$C_u = u\%' / (u\%' + 200) \quad (3a)$$

for the upper threshold, and

$$C_l = l\%' / (l\%' + 200) \quad (3b)$$

for the lower threshold.

The above transformation constrains the absolute values of C_u and C_l to be always the same. Thus the contrast threshold can be fully represented by only one of them. Because the phase of the diagonal Fourier components is shifted by 180° in the two threshold conditions, C_l will be equal to $-C_u$.

There is evidence (Campbell and Robson, 1968) that the detection of a complex waveform (e.g. square-wave) grating is determined by the contrast of

its fundamental Fourier component. As in the plaid pattern all diagonal Fourier components add up to a triangular-wave, the contrast of only the fundamental Fourier component will be $8/\pi^2$ (0.81) times the contrast of that triangular wave. In order to compare the contrast threshold values of this study with those found by other investigators, the contrast threshold values have been corrected for the fundamental Fourier component. The threshold contrasts for the checkerboard fundamental components (C_{tf}) were finally determined by the following equations:

$$\begin{aligned} C_{tf} &= u\%/(u\%+200) \cdot 8/\pi^2 \\ &= - l\%/(l\%+200) \cdot 8/\pi^2 \end{aligned} \quad (4)$$

Chapter III

RESULTS AND DISCUSSION

3.1 White-Light Data

3.1.1 Deviation from a Logarithmic Prediction

The dependence of the thresholds for the presence of an afterimage grid on pattern-average luminance and contrast is shown in *Figs.7* and *8*, respectively. In *Fig.7* the data of the three subjects have been plotted against pattern-average luminance (abscissa) and in *Fig.8* against pattern contrast. All threshold values are expressed in terms of the percent deviation of the grey squares with respect to the geometric mean of the black and white squares (ordinate). For the sake of clarity this measure will be called the *deviation from a logarithmic prediction*. In both figures, the columns always consist of data obtained from the same subject. In *Fig.7* the rows of data plots all refer to the same pattern contrast, whereas in *Fig.8* they refer to the same pattern-average luminance. For the rows, only every second contrast or average luminance condition tested is shown.

The upper curve in the single plots represents the upper (bright grey squares) and the lower curve the lower (dim grey squares) threshold values for the presence of the afterimage grid. The curves in between are the geometric means of the upper and lower thresholds. The shaded area indicates the conditions for which no diagonal afterimage grid could be generated. Although the distance between the upper and the lower threshold values was often quite large, the transition from the 'no-afterimage' to the afterimage condition usually occurred within a range of only 1-3% of the

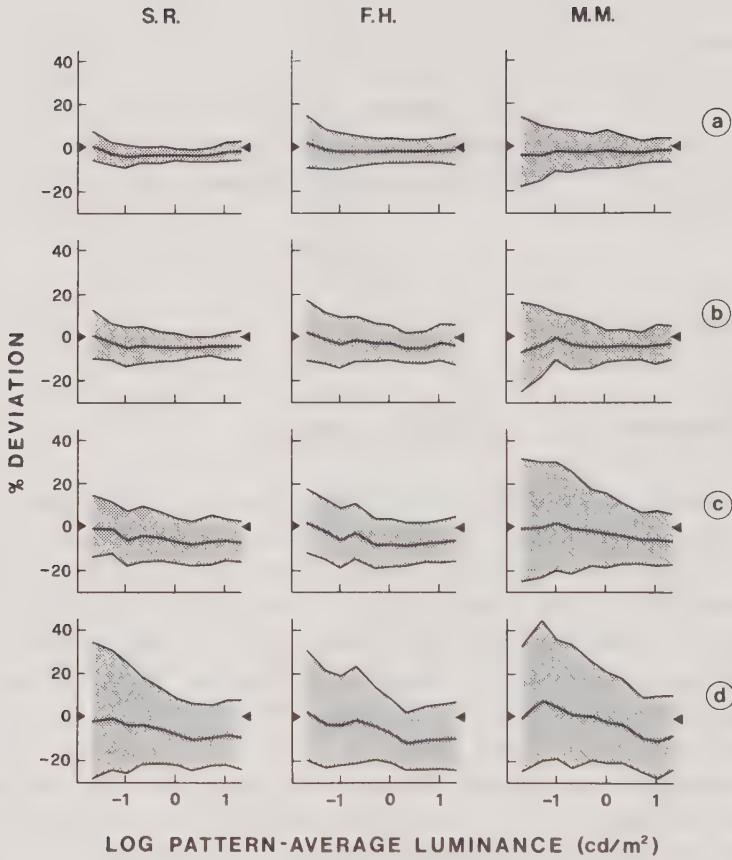


Fig. 7: Thresholds for the presence of an afterimage grid as a function of pattern-average luminance.

abscissa: log pattern-average luminance

ordinate: % deviation from a logarithmic prediction

rows (a-d): pattern contrast; 0.2, 0.4, 0.6 and 0.8, respectively

columns: subjects S.R., F.H. and M.M.

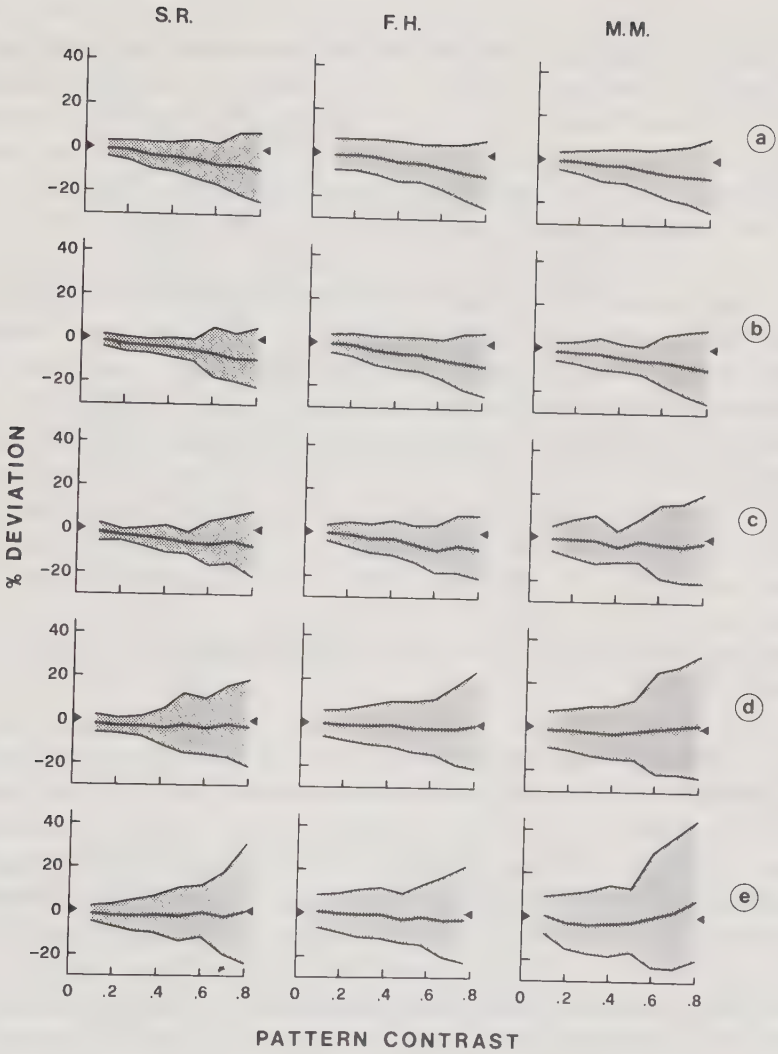


Fig. 8: Thresholds for the presence of an afterimage grid as a function of pattern contrast.

abscissa: pattern contrast

ordinate: % deviation from a logarithmic prediction

rows (a-e): pattern-average luminance; 22, 5.5, 1.1, 0.22, 0.055 cd/m^2 , respectively.

columns: subjects S.R., F.H. and M.M.

grey square's absolute luminance. The standard deviation for the threshold values was normally less than 1% and never exceeded 2%. Because of their relatively small magnitude, standard deviations have not been included in the data plots. The two arrows on the left and the right side of each data plot indicate the 0% deviation line. If luminance transduction were perfectly logarithmic, the mean deviation data (middle curve) would lie on a horizontal line connecting these arrows.

A common feature of the data shown in *Figs.7* and *8* is that generally the mean deviation from a logarithmic prediction is quite small. The largest mean deviations (around -10%) are found in all subjects under high pattern contrasts (0.8) and moderate luminance conditions (5.5 to 22 cd/m², 0.74 to 1.35 log cd/m²). A quick glance at the general form of the deviation data under different pattern contrasts and average luminances shows that it is quite similar for subjects S.R. and F.H., but that it is quite different for subject M.M. for lower pattern-average luminances. There seems to be a good reason for this difference, which will be discussed below. On the basis of data obtained with two other subjects in a preliminary pilot study, the data of S.R. and F.H. can be considered representative of the normal case.

A common property of the upper and lower threshold curves is their systematic asymmetry with respect to the 0% deviation line. For this reason the mean deviation values tend to be negative. With an increase in pattern contrast as well as in average luminance, the mean deviation from a logarithmic prediction becomes more and more negative. Under low pattern contrast or average luminance conditions the mean deviation is very close to 0%.

The data plots not only provide a measure of how well the visual system performs in comparison to a perfect logarithmic transducer, they also provide a measure of its sensitivity. This is given by the separation of the upper and lower threshold values. The larger the separation between the threshold values, the brighter or darker the relative luminances of the grey squares had to be in order to generate an afterimage grid. In this sense a large separation means that the sensitivity of the visual system for detecting the diagonal Fourier components of the checkerboards is relatively low and vice versa.

In *Fig.7* a decrease in the pattern-average luminance is accompanied only by a small increase in separation between the threshold values, except perhaps at higher pattern contrasts. The separation reaches a minimum at pattern-average luminances between 2.2 and 5.5 cd/m^2 (0.34 and 0.74 $\log \text{cd/m}^2$).

Compared to a variation in pattern-average luminance, a change in pattern contrast (*Fig.8*) produces considerably larger changes in sensitivity. In most cases the sensitivity decreases smoothly from the lowest pattern contrast (0.1) up to pattern contrasts of about 0.5. For higher pattern contrasts (0.6 to 0.8) the decrease in sensitivity seems to change more rapidly. Thus the area enclosed by the two threshold curves closely resembles the shape of a trombone, with its bell-shaped mouth pointed toward higher pattern contrasts.

3.1.2 A closer Look

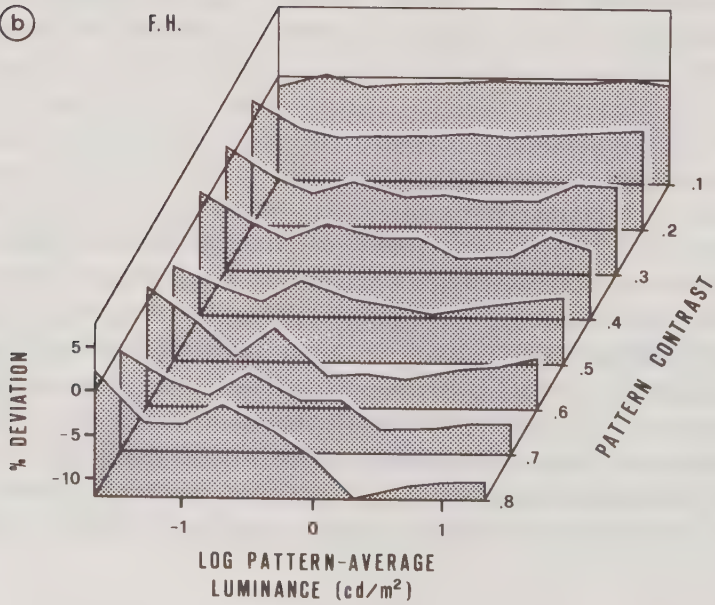
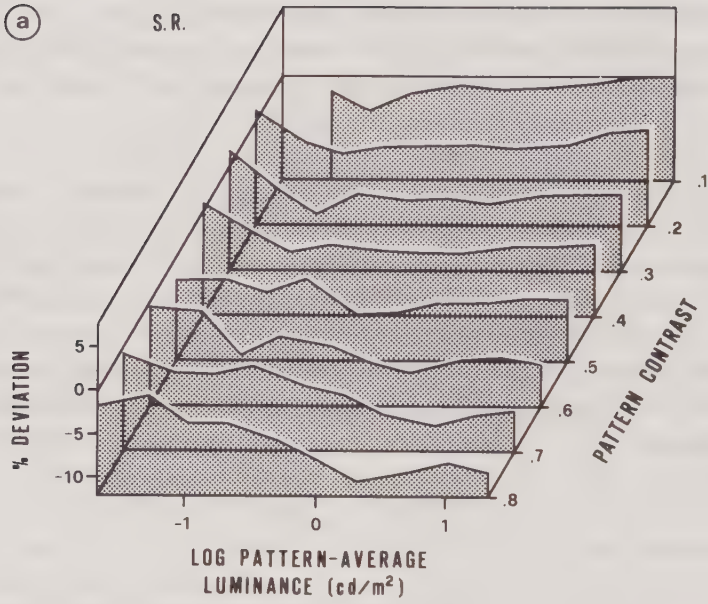
A more detailed 2 1/2-D plot of the mean deviations from a logarithmic prediction is given in *Fig.9a-c*. The pattern-average luminance is plotted along the abscissa; and curves of the same pattern contrast are depicted along the depth dimension. The bottom plane of the graphs represents -12% deviation and the 0% deviation plane is indicated by the two lines drawn on the sideplanes.

In addition to the properties discussed above, this enlarged view of the mean deviation data reveals three new aspects:

First of all, the mean deviations found for plaid patterns with an average luminance above 2.2 cd/m^2 (0.34 $\log \text{cd/m}^2$) appear to remain fairly constant within a specific pattern contrast. There is nevertheless a slight tendency for the mean deviations to decrease with higher luminances.

Second, for higher pattern contrasts, a fast rise toward 0% deviation can be observed at pattern-average luminances below 2.2 cd/m^2 . With lower pattern contrasts this rise is less pronounced because even the starting values at higher pattern-average luminances do not show large deviations.

Third, in subjects S.R. and F.H. the approach toward 0% deviation is interrupted by a return to larger negative deviations at pattern-average



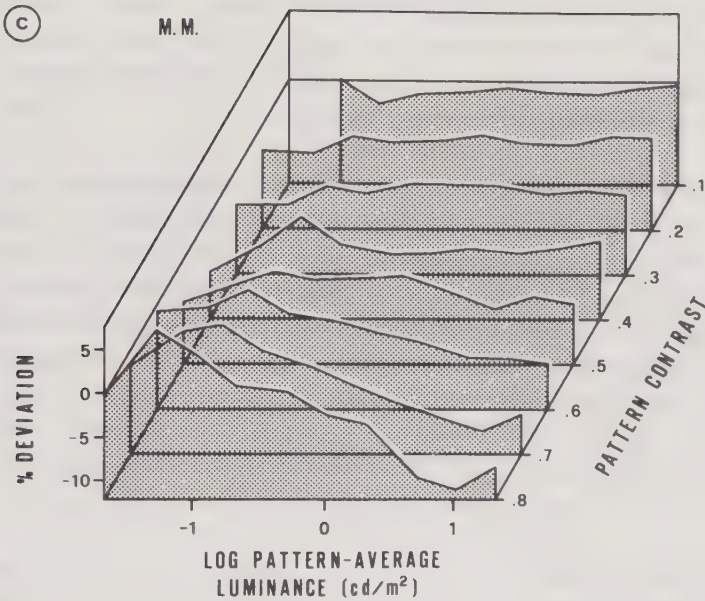


Fig. 9: Mean deviation from a logarithmic prediction.
 abscissa: log pattern-average luminance
 ordinate: % deviation from a logarithmic prediction
 depth dimension: different pattern contrast conditions
 subjects: S.R. (a), F.H. (b), M.M. (c)

luminances near 0.1 cd/m^2 . This discontinuity can be observed for all pattern contrasts. At lower pattern average luminances their data curves rise again toward the 0% deviation line.

This, however, is not true for subject M.M.. At the higher pattern contrasts his curves start earlier to move toward smaller deviations, while at the lower pattern-average luminances large positive deviations can be observed. Most of his curves return to smaller positive or negative devia-

tion values at the lowest pattern-average luminances tested. Thus, the data for subject M.M., obtained under lower luminance conditions, display the opposite pattern to what was found for the other two subjects. Specifically, the 'dip' of negative deviations around 0.1 cd/m^2 observed in these subjects stands in contrast to a peak of positive deviations in subject M.M. at the same pattern-average luminance.

What is the reason for this difference? A pattern-average luminance of 0.1 cd/m^2 lies in the neighbourhood of the transition from mesopic to scotopic vision. The discontinuity observed in the deviation data might therefore be related to the change from predominantly cone to rod mediated vision. This hypothesis was tested by repeating some of the white-light experiments under long wavelength (red-light) conditions. With red-light, the contribution of the rod system is reduced and the plaid pattern is primarily processed by the cone system. Before presenting these data in the next section, I would like to describe some other aspects of the white-light data.

3.1.3 Diagonal Contrast

As already mentioned in the method section the representation of the threshold data in terms of the deviation from a logarithmic prediction is a very sensitive one. This is because the data are already plotted relative to a logarithmic base function. In order to get a better feel for the entire 'signal' produced by the non-linear transduction of luminance, the threshold values have been converted to *diagonal contrast* values. Diagonal contrast (C_d) was defined as the Michelson contrast of the black (b) and white (w) squares' average with respect to the grey squares (g):

$$C_d = \frac{(b + w)/2 - g}{(b + w)/2 + g} \quad (5)$$

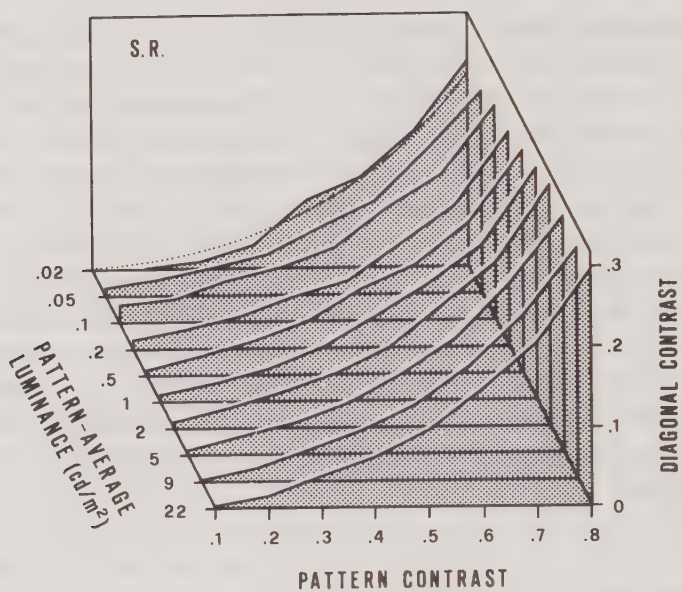
To eliminate the afterimage, the luminance of the grey squares has to be changed to a value that corresponds to the 'physiological' mean of the black and white squares. If any kind of non-linearity is present in the visual system, this value will never coincide with the arithmetic mean of the black and white squares. A plaid pattern at the 'physiological balance point' (no afterimage) will therefore always contain the diagonally oriented fundamental Fourier components of a checkerboard in the physical domain. The contrast of these components will rise in proportion to the pattern contrast. This is because the closer two luminance values are together, the better a nonlinear function can be approximated by a linear one. In other words, the smaller the contrast between the black and white squares of the plaid pattern, the closer the nonlinear mean will correspond to the linear, arithmetic mean. The values for the physical diagonal contrast of a plaid pattern, not accompanied by an afterimage, are therefore expected to increase with pattern contrast, if the transducer function is non-linear.

In *Fig.10a-c* the mean of the physical diagonal contrast at the upper and lower threshold is plotted against the pattern contrast. Along the depth dimension different pattern-average luminance conditions are depicted. The expectancy that the amount of physical diagonal contrast needed to balance out the effects of a non-linear transduction, increases with pattern contrast is clearly fulfilled: Diagonal contrast steeply accelerates with increasing pattern contrast. At all pattern-average luminances, the shape of the curves remains more or less the same.

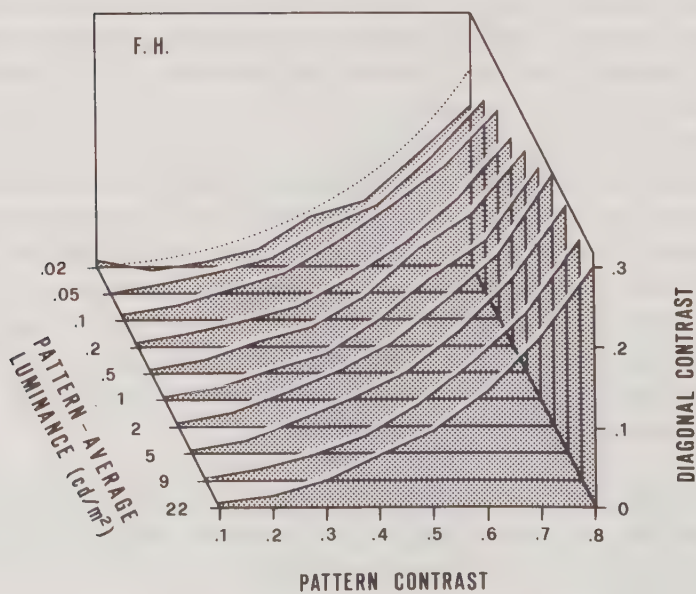
If luminance transduction in the visual system were linear, all data should lie on a horizontal line at zero diagonal contrast. The hypothetical course of diagonal contrast values with a perfect logarithmic transducer is given by the dotted curve in each plot. The data do in fact match this hypothetical log-transduction characteristic very well. The best correspondence is given by the data curves obtained under the lower pattern-average luminance conditions. This is to be expected because the deviation data also show a minimum under these conditions.

The smoothness of the data curves in *Fig.10* reflect the high accuracy of the psychophysical method used. As the standard deviation bars would not be much larger than the thickness of the curves, they have not been included in the plots.

(a)



(b)



(c)

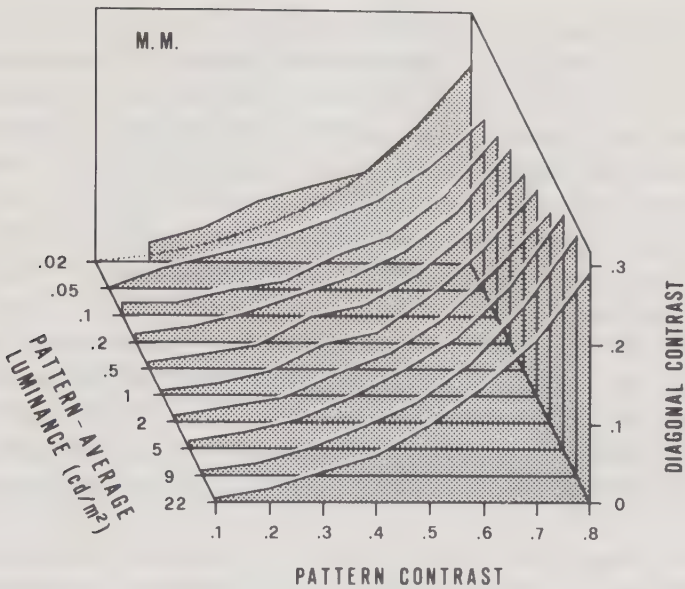


Fig. 10: Diagonal contrast of the plaid pattern at the 'balance point'.
 abscissa: pattern contrast
 ordinate: diagonal contrast
 depth dimension: different pattern-average luminances
 subjects: S.R. (a), F.H. (b), M.M. (c).

At low pattern contrasts the diagonal contrast values are so small that a linear transduction can hardly be distinguished from a non-linear one. It has to be kept in mind that high pattern contrast conditions determine the specificity of the underlying transducer function in a much more significant way.

3.1.4 Contrast Thresholds

According to *Equation 4* (see Methods) sensitivity can be expressed in terms of the contrast of the checkerboard fundamental Fourier components required to produce the upper and lower thresholds. For any contrast between these two threshold contrasts, the visual system is presumably not able to detect the diagonal checkerboard Fourier components. As a consequence, there will be no diagonally oriented afterimage within this region. Relatively small contrast threshold values indicate that the visual system is able to detect even small deviations from a 'physiologically balanced' plaid pattern. The opposite holds for larger contrast thresholds. As the contrast values for the upper and lower thresholds will be the same, except for their sign, the contrast threshold for the checkerboard fundamental Fourier components can be represented by a single value. The change of sign is due to the fact that, with respect to the upper and lower threshold, the fundamental Fourier components of the checkerboard have opposite phase.

There still remains the problem about how to interpret the calculated contrast thresholds. On the one hand, the thresholds are certainly contrast detection thresholds for the checkerboard fundamental Fourier components. On the other hand, they were determined with suprathreshold plaid patterns. Thus the experimental situation was quite different from a mere contrast detection task: In fact, the checkerboard fundamental components had always be detected *against* a suprathreshold plaid pattern. Depending on the pattern contrast, this plaid pattern may have *masked* the checkerboard components by varying amounts. Thus the calculated thresholds would seem to more closely represent *contrast discrimination* thresholds. However, it should not be forgotten that, in the standard contrast discrimination experiment, differences in contrast have to be detected in gratings of the same spatial frequency and orientation. In the present investigation, on the other hand, the fundamental Fourier components of the checkerboard are an integral part of the pattern itself. In addition they have a different orientation (diagonal) and spatial frequency than the ordinary plaid pattern Fourier components. Nevertheless, despite these caveats, the contrast threshold data, which will be presented on the following pages, reveal striking similarities with the contrast discrimination thresholds found by other investigators.

3.1.5 Contrast Thresholds for different Pattern-Average Luminances

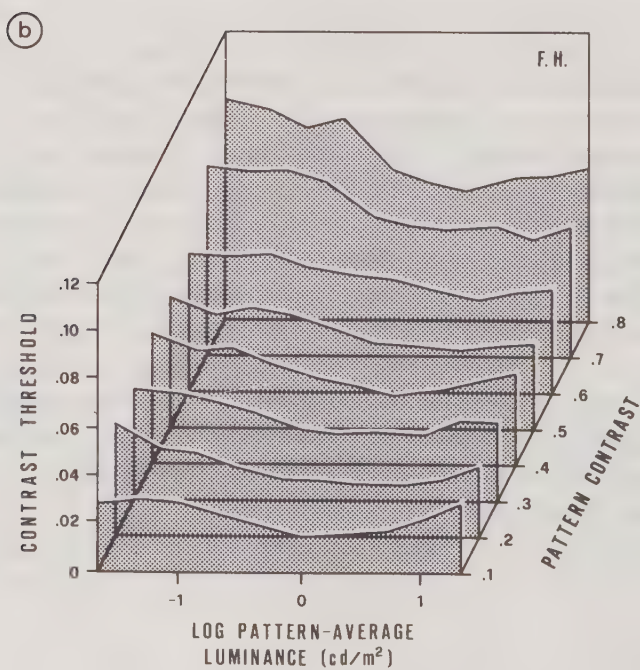
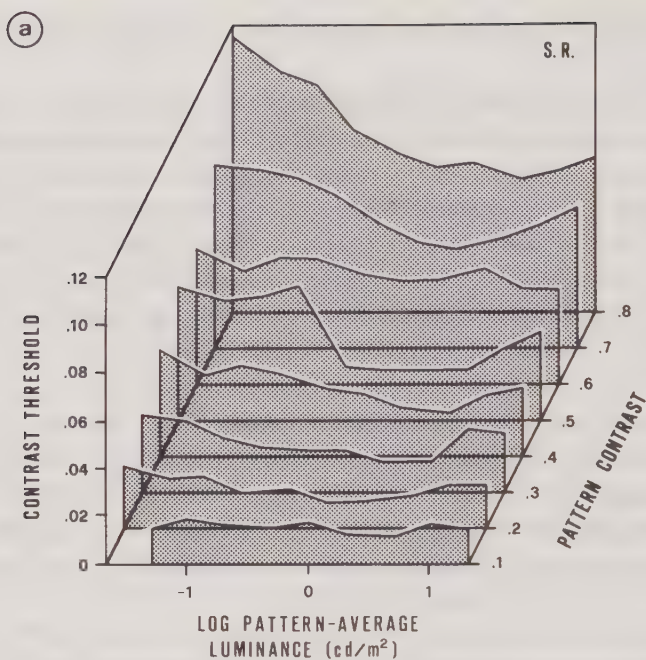
In *Fig.11a-c* the calculated contrast thresholds for the checkerboard fundamental components are plotted against the pattern-average luminance. Data curves of different pattern contrast are depicted along the depth dimension. At the highest pattern-average luminance, the threshold values for subject S.R. and F.H. (*Fig.11a and b*) first decrease reaching a minimum near 2 cd/m^2 ($0.3 \log \text{ cd/m}^2$). At lower pattern-average luminances, their contrast thresholds increase again until, at very low luminance values, they seem to reach a more or less constant value.

The threshold data of subject M.M. deviate from this pattern in two aspects: First of all, the increase in contrast threshold with decreasing pattern-average luminance is much steeper than in the other two subjects. Second, most of M.M.'s data curves do not reach a steady plateau at very low pattern-average luminances. Yet, at higher luminances the contrast thresholds of M.M. are comparable to those of the other two subjects.

The fact that the differences in M.M.'s contrast thresholds also seem to be restricted to lower luminance levels, suggests once again that the cone-rod transition is somehow responsible for his anomalous data.

The contrast threshold data of subject S.R. and F.H. compare well with the contrast discrimination thresholds reported by Kohayakawa (1972) for sine-wave gratings. He also found that the contrast discrimination thresholds rise in the region of near 1 cd/m^2 . His absolute values, however, are generally higher than those found in the present study. This may be because he used the method of adjustment, which is known to yield higher threshold values. The ratio of the threshold values at 0.1 and 2 cd/m^2 , which is about 1.6, is very nearly the same for Kohayakawa's contrast discrimination data and for the contrast thresholds obtained in this investigation.

It is interesting to note that threshold ratios of the same magnitude can be calculated from the *contrast sensitivity* data obtained with sinewave gratings of comparable luminance and spatial frequency (Daitch and Green, 1969; van Meeteren and Vos, 1972).



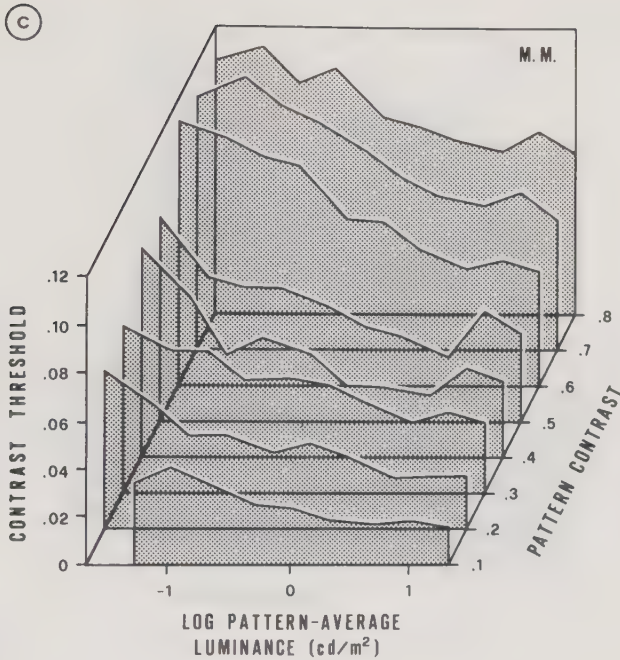
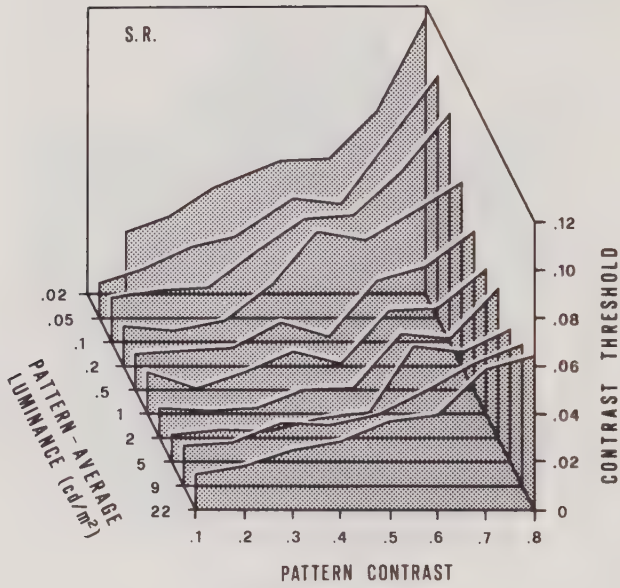


Fig. 11: Contrast thresholds for the checkerboard fundamental components as a function of pattern-average luminance.
 abscissa: pattern-average luminance
 ordinate: contrast thresholds
 depth dimension: different pattern contrast conditions
 subjects: S.R. (a), F.H. (b), M.M. (c)

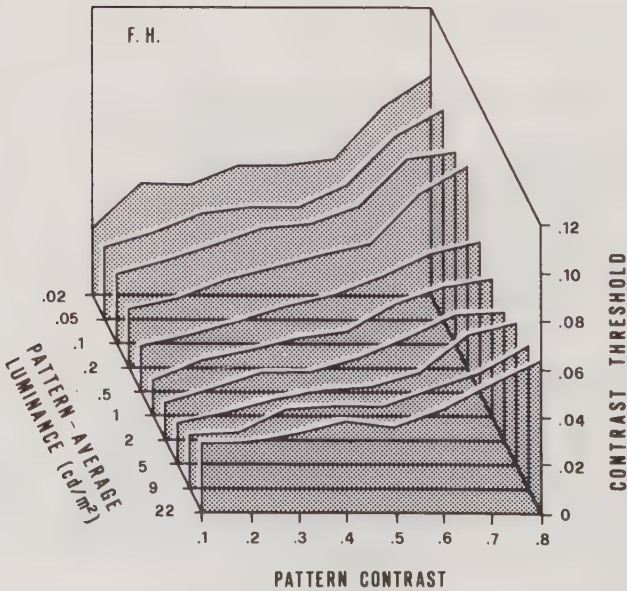
3.1.6 Contrast Thresholds for different Pattern Contrasts

Up to this point only the contrast thresholds measured for different pattern-average luminances have been considered. The contrast threshold data depicted in *Fig. 12a-c* are identical with those of *Fig. 11a-c*, except that the angle of view has been changed. Now the calculated contrast thresholds

(a)



(b)



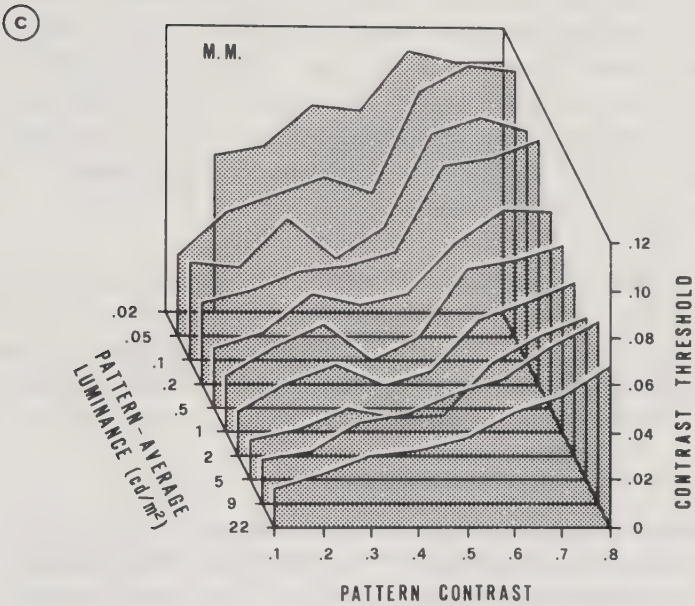


Fig. 12: Contrast thresholds for the checkerboard fundamental components as a function of pattern contrast.

abscissa: pattern contrast

ordinate: contrast thresholds

depth dimension: different pattern-average luminance conditions

subjects: S.R. (a), F.H. (b), M.M. (c)

for the checkerboard fundamental components are plotted against the pattern contrast and data curves of the same pattern-average luminance are plotted along the depth dimension.

The most prominent feature of all the data curves is the rise in contrast threshold with increasing pattern contrast. For lower to moderate pattern-

average luminances ($0.5 - 22 \text{ cd/m}^2$), the contrast thresholds rise very slowly, increasing their slope slightly at higher pattern contrasts ($0.6 - 0.8$). At very low luminances ($0.022 - 0.22 \text{ cd/m}^2$), this region of increasing slope is more pronounced and is also shifted toward higher pattern contrasts. In subjects S.R. and M.M. a return to lower contrast thresholds can be observed at pattern contrasts of about 0.4 to 0.6 . At lower pattern-average luminances the dip in the threshold curves appears to be shifted towards higher pattern contrasts.

A very similar non-monotonicity in contrast discrimination thresholds has also been observed by Kohayakawa (1972). His thresholds first rise smoothly up to a pattern contrast of 0.25 and then moderately decrease again. Because Kohayakawa tested only pattern contrasts up to 0.35 , it remains unclear if his threshold data would show a rise again at higher pattern contrasts.

A comparison of the contrast threshold data obtained in the the present investigation and the contrast increment thresholds obtained by Legge (1981) with sinewave gratings is given in *Fig.13*. Legge postulates a power law for contrast discrimination and therefore plots his data in log-log coordinates. The straight line in *Fig.13* corresponds to the best power function fit of Legge's data. It has a slope of 0.59 . The symbols are the contrast thresholds calculated for the three subjects in this investigation at a comparable pattern average luminance. Except perhaps for a pattern contrast of 0.1 , the contrast thresholds for subject S.R. and F.H. match very well the contrast discrimination thresholds measured by Legge. Slightly higher thresholds can be observed for subject M.M., whose data seem to be shifted upwards by a more or less constant factor.

The goodness of fit between Legge's and my data at comparable pattern contrasts seems to indicate that a power function provides an adequate representation of both our data for the pattern contrast range given in *Fig.13*. However, if one considers the contrast threshold data for the whole range of pattern contrasts tested, one can hardly assume a power function to be an appropriate representation. First, the contrast thresholds increase again steeply beyond a pattern contrast of 0.6 . Second, the discontinuity observed at pattern contrasts of about 0.4 to 0.6 (see *Fig.12*)

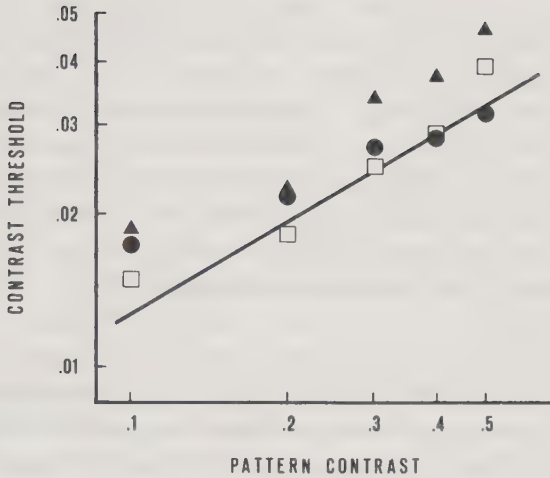


Fig. 13: Contrast thresholds for the checkerboard fundamental components and the power law for contrast discrimination suggested by Legge (1981).

The contrast thresholds are plotted against pattern contrast in log-log coordinates. The symbols correspond to the data obtained for subjects S.R. (□), F.H. (●) and M.M. (▲). The solid line is the best fitting power-function suggested by Legge for his contrast discrimination thresholds.

indicates that the dependence of the contrast thresholds on the pattern contrast can not be satisfactorily described by a monotonously increasing function. In the literature only Kohayakawa (1972) has described a similar non-monotonicity of contrast discrimination thresholds (see above). The reason why other investigators do not report such a behavior in their data, may be either because the sampling of pattern contrasts was too coarse or because the non-monotonicity was discounted as noise. Indeed, a closer look at the data of Legge (1981) reveals a return of some of his contrast discrimination thresholds to lower values at a pattern contrast of about 0.5.

For the present study it is also important to note that the return to lower contrast thresholds at pattern contrasts around 0.5 is not found for every pattern-average luminance condition, and that it characteristically differs for the three subjects. However, a common feature of the contrast threshold data under all pattern-average luminances and for all subjects is a discontinuity in slope at this particular pattern contrast (see *Fig.12*). Thresholds seem to increase up to a pattern contrast of about 0.3. For pattern contrasts between 0.3 and 0.5, the thresholds almost remain constant. Above 0.5, however, they steeply increase again.

So far, the contrast threshold data have only been presented and described. It remains to be explained what underlying mechanisms make the present data so comparable with the results obtained in ordinary contrast discrimination experiments. This is related to the more specific question of why the contrast thresholds increase with higher pattern contrasts. The afterimage method used here is so different from standard experiments on contrast discrimination that it seems to be rather difficult to make such a connection.

Yet, there is an attractive hypothesis, based on the specific shape of the transducer function, which not only opens the possibility of a direct comparison, but also provides an explanation for the observed similarity. Since up to this point, it has only been assumed that the transducer function has quasi-logarithmic properties, a detailed treatment of this issue must be postponed until the specific shape of the transducer function is inferred from the experiments conducted under long-wavelength conditions.

3.2 Red-Light Data

3.2.1 Preliminary Considerations

In order to test the hypothesis that the oddities in the deviation data (*Fig.10a-c*) observed at lower pattern-average luminances are related to the cone-rod transition, some of the experiments were repeated under red-light conditions (filter RG-630, Schott). Although at 630 nm the sensitivity of the rod system is comparable to that of the cone system in absolute terms, the sensitivity of the rods at this wavelength relative to its peak is reduced by about 2 log-units (Wald 1945). However, the question which photoreceptor system is processing the plaid pattern depends not only on the spectral luminosity functions of the rods and cones, but also on the pattern-average luminance. At higher luminance levels the rod system saturates and therefore can not be considered to contribute to the processing of the pattern at all. Under mesopic light conditions, both the rod and the cone system are active, but longer wavelength stimuli will bias the response in favor of the cone system. It is difficult to estimate the exact extent of bias, but it can be safely assumed that the thresholds measured with the red-light plaid patterns were mainly being determined by the cone system.

3.2.2 Deviation from a Logarithmic Prediction

The mean relative luminance of the grey squares, for which no afterimage was present, is again expressed in terms of the deviation from a logarithmic prediction (= geometric mean of the black and white squares in the plaid pattern).

In *Fig.14a* (F.H.) and *14b* (M.M.) this mean deviation is plotted against pattern-average luminance for pattern contrasts of 0.5 and 0.7. The deviations from a logarithmic prediction for the red-light condition are represented by the filled circles. For comparison the data obtained under white light conditions are included in the plots and indicated by the open squares.

At the high end of the pattern-average luminance range tested there is almost no difference between the response pattern obtained under the red-

light and white-light conditions. With decreasing average luminance the red-light data accelerate steeply and reveal large positive deviations from the logarithmic prediction, which peak around 0.1 cd/m^2 .

For the red-light condition these two subjects show almost identical characteristics. This stands in contrast to the substantial differences found between these two subjects with white-light stimulation at lower pattern-average luminances. There, the deviations of subject F.H. become more negative in a dipper-shaped fashion, whereas the data of subject M.M. show a peak at the same location.

Although the deviation data demonstrate how well the visual system approximates a perfect logarithmic transducer, the exact form of the transducer function for luminance still remains to be clarified. Since the mean of the upper and lower threshold luminances for the grey squares can be regarded as the luminance 'physiologically' located midway between that of the black and white squares, it is possible to reconstruct the transducer function according to this information. If, for example, the luminance of the grey squares were always the arithmetic mean of the black and white squares the transducer function would be a linear one. On the other hand, if the luminance were always the geometric mean, it would be a logarithmic one instead. The data, however, do not reveal a simple linear or logarithmic relationship and the shape of the underlying transducer function is assumed, therefore, to be more complex.

There is a lot of neurophysiological evidence that the intensity transducer function of retinal receptors is S-shaped and that it can be described by the following equation:

$$H(I) = \frac{I^n}{I^n + \sigma^n} \quad (6)$$

where I is the intensity of the stimulus, σ the half-saturation constant and n an exponent with a value usually between 0.7 and 1.0 (Naka and Rushton 1966; Dowling and Ripps, 1971, 1972; Baylor and Hodgkin, 1974; Norman

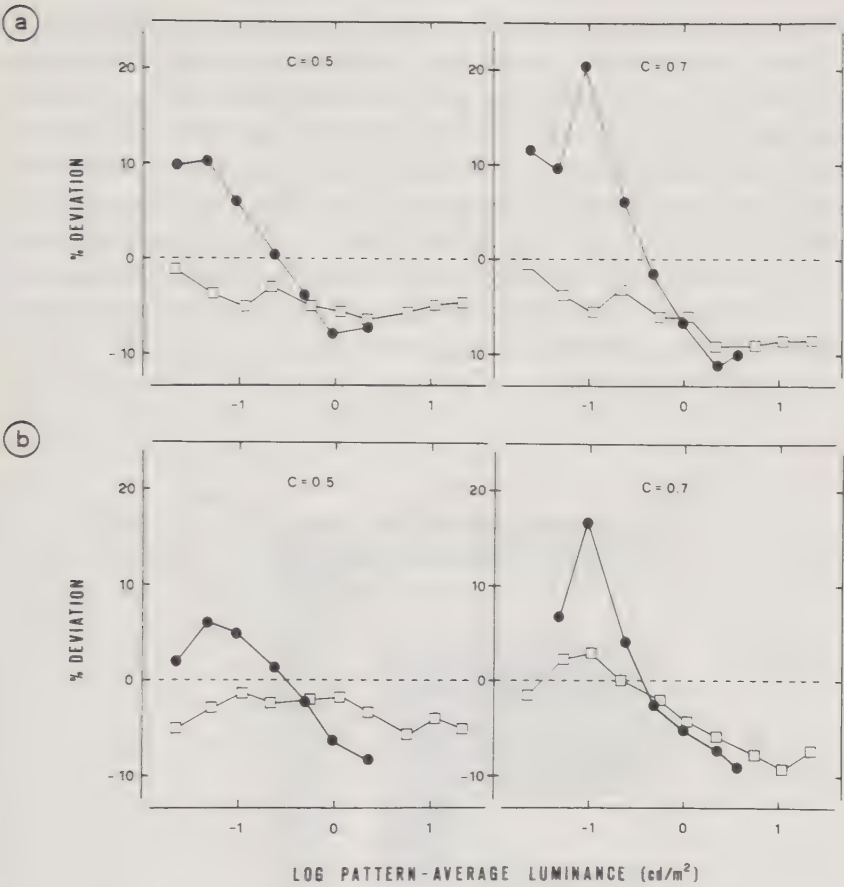


Fig. 14: Mean deviations from a logarithmic prediction as a function of pattern-average luminance for subjects F.H. (a) and M.M. (b). Two pattern contrast conditions (0.5 and 0.7) are shown. The filled circles (●) are the data obtained under red-light conditions. For comparison the corresponding white-light data (□) are added to the figures.

and Werblin, 1974; Kleinschmidt and Dowling, 1975; Fain, 1976; Valetton and Norren, 1983). This function has also been termed a H-function because in the log-domain its shape is similar to that of a hyperbolic tangent (mathe-

matically it is of course not strictly correct to use the term hyperbolic for such a function). In *Fig. 15* a H-function with an exponent of 1.0 is plotted against log-intensity. The value for the half-saturation constant is indicated by the arrow on the intensity axis. The H-function can be characterized as having a segment of increasing slope below the half-saturation point and a segment of decreasing slope for intensity values above it (saturation). In the log-domain the function is almost linear around the half-saturation point. This implies that luminance processing is quasi-logarithmic in this region. At the lower tail of the function it will be less compressive and at the upper end more compressive than a logarithm.

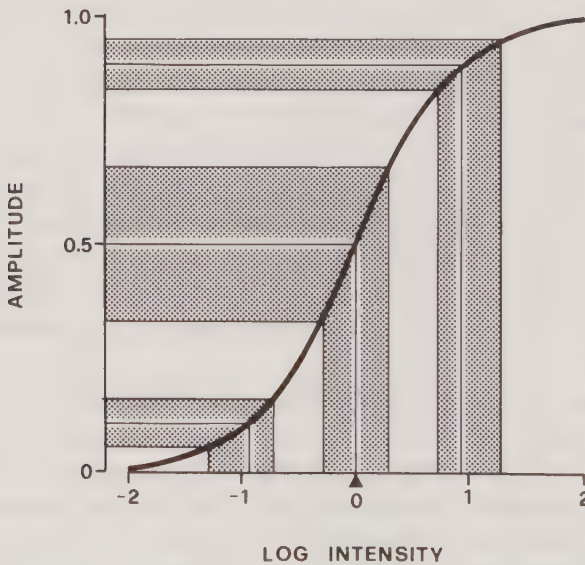


Fig. 15: The H-Function.
(see text)

Such a characteristic is in fact well in accord with the course of the deviations from a logarithmic prediction found for the red-light condition. In

Fig.15 this is demonstrated by constructing an intensity value which gives a response just midway between those of two other intensity values. For two intensity values placed around the half-saturation point, the intensity giving a response between them will correspond exactly to the geometric mean of the two values. The deviation of this value from the calculated geometric mean of the two surrounding intensities will therefore be 0%. For two intensity values located at the upper end of the H-function the intensity value giving a midway response will be lower than the geometric mean. The opposite holds for the lower tail of the H-function. In other words, at the upper end of the H-function, one would expect negative deviations from a geometric mean; whereas at the lower tail, the deviations should be positive. This is exactly what has been found for the red-light deviation data of this investigation (compare *Fig.14a* and *b*).

A more complete description of the deviations from the geometric mean expected according to an H-function is given in *Fig.16*. The deviation values have been calculated for three different pattern contrasts (0.3, 0.5 and 0.7) according to the following set of equations:

$$H(g_m) = \frac{H(w) + H(b)}{2} \quad (7a)$$

$$g_m = \frac{H(g_m) \cdot \sigma}{1 - H(g_m)} \quad (7b)$$

$$d\% = \left[\frac{g_m}{\sqrt{w \cdot b}} - 1 \right] \cdot 100 \quad (7c)$$

By applying a H-function, the intensity (g_m) which gives a response midway between those of two other intensities (b and w) can be calculated from *Equations 7a* and *7b*. The corresponding deviation ($d\%$) from a logarithmic prediction is given by *Equation 7c*. In the case of the plaid pattern b , w and g_m would be the luminance of the black, white and grey squares, respectively. If only pattern contrast (C), pattern-average luminance (L_a), and half-saturation constant (σ) are given, the values for b , w , g_m and $d\%$ can be calculated from the following equations:

$$w = \frac{\sigma - L_a - \sqrt{(L_a - \sigma)^2 - 2L_a \cdot \sigma \cdot (C^2 - 2)}}{C^2 - 2} (1 + C) \quad (8a)$$

$$b = \frac{1 - C}{1 + C} \cdot w \quad (8b)$$

$$d\% = \left[\frac{2L_a(1 - C) - w}{w\sqrt{1 - C^2}} - 1 \right] \cdot 100 \quad (8c)$$

$$g_m = \sqrt{b \cdot w} + \sqrt{b \cdot w} \cdot d\% / 100 \quad (8d)$$

The half-saturation constant (σ) of the H-function depicted in *Fig.16* (dotted curve) has been set to unity. Therefore the hypothetical deviations from a logarithmic processing of luminance are given relative to pattern-average luminances that are higher or lower than this half-saturation value. As expected the sign of the calculated deviation is negative for pattern-average luminances above and positive for those below the half-saturation point. The deviation curves look almost like mirror images of the H-function around the abscissa. The amplitude of the hypothetical deviation curves is proportional to the pattern contrast in the sense that for higher pattern contrasts the deviations are larger than for lower ones. This is to be expected because for very low pattern contrasts the H-function or any other smooth function can be approximated by a linear function. As for small luminance differences (i.e. low pattern contrasts), the geometric mean will be almost equivalent to the arithmetic mean, the deviation values must necessarily decrease with lower pattern contrasts.

A comparison of these hypothetical deviation values with the deviation data obtained under red-light conditions reveals a remarkable similarity. First of all, the sign of the deviation values seems to accord with the hypothetical curves. Second, the deviations found for higher pattern contrasts are indeed larger than those for lower ones. Third, the slope of the experimental deviation curves around the 'sign inversion point' is almost the same as found for the hypothetical deviations.

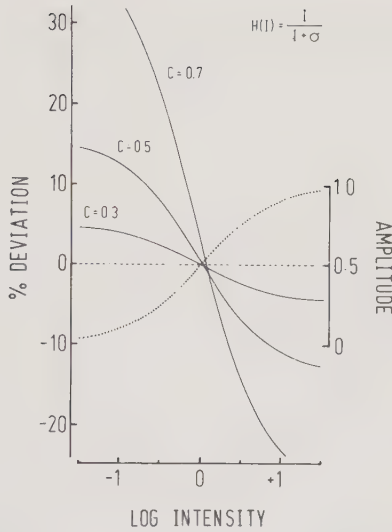


Fig. 16: Hypothetical deviations from a logarithmic prediction based on a H-function.

A demonstration of this correspondence is given in *Fig.17a* (F.H.) and *17b* (M.M.), where the best fitting hypothetical deviation function is plotted together with the experimental data (symbols). For reasons that will be explained in detail below, only the data marked by a small horizontal dash were used for the optimal fitting procedure (method of least squares). The best fit of the hypothetical deviation curves to the experimental data was done by adjusting the half-saturation constant (σ) and the exponent (n) of the H-function. If an exponent is introduced, *Equations 9a-c* have to be modified slightly. In addition a two step iterative algorithm has to be added to the calculation procedure in order to ascertain a constant pattern-average luminance. The optimal exponent was determined on the basis of the 0.5 contrast data and was found to be 0.98 for subject F.H. and 0.85 for M.M.. For a pattern contrast of 0.5 (open squares), the optimal half-saturation constant was 0.28 cd/m² for subject F.H. and 0.29 cd/m² for subject M.M.. For a pattern contrast of 0.7 (filled circles), the half-saturation constant values were 0.23 cd/m² for F.H. and 0.25 cd/m² for M.M.. The optimal half-saturation constants are indicated by an arrow on the abscissa.

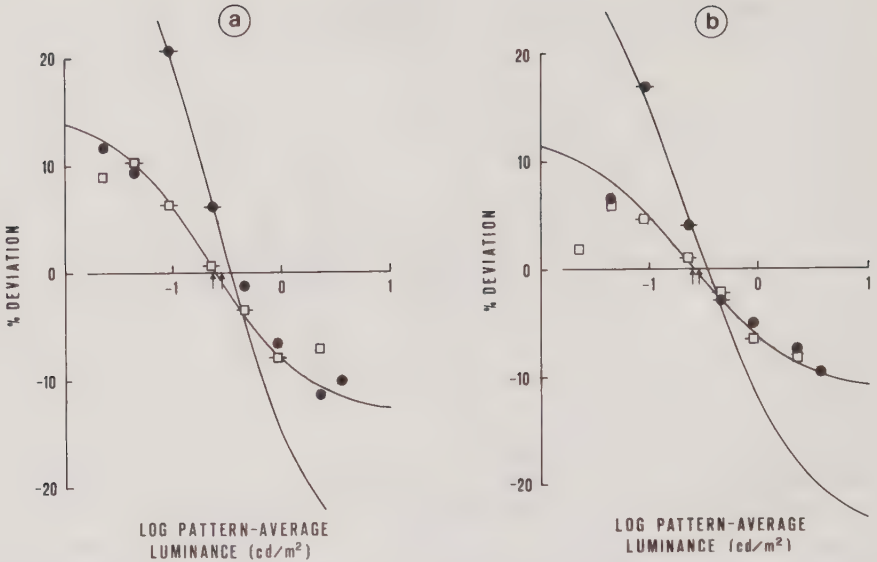


Fig. 17: The best-fitting deviation functions according to a H-function. The plots show the data for subjects F.H. (a) and M.M. (b) and for pattern contrasts of 0.5 ($\square$) and 0.7 ($\bullet$). The arrows indicate the values of the half-saturation constants for the best fitting H-functions.

Although the experimental deviation data match the hypothetical deviations based on a H-function very well in the region of the half-saturation constant and in a limited range below that value, considerable differences can be observed for the lowest and highest pattern-average luminances tested. The reason why there are differences at lower pattern-average luminances is probably that the cone signal becomes so weak that, even under red-light conditions, a contribution of the rods to the processing of the pattern can not be excluded. The luminance transducer function of the rods is also considered to be a H-function (Fain and Dowling 1973), but with a half-saturation constant about 1.4 log-units below that of the dark adapted cones. Thus the lowest pattern-average luminance tested in this investigation would be close to the value of the half-saturation constant of the rods (assuming that the half-saturation constant of the cones is about 0.25

cd/m^2). If this assumption is true the pattern at this level would have been processed by a receptor system (rods) whose half-saturation constant is close to the pattern-average-luminance. A return toward smaller deviation values would be expected because the transduction characteristic is then close to a logarithm.

For moderate and higher pattern-average luminances, adaptational mechanisms are most likely responsible for the differences observed between the simulated and real deviation data. The present conception of these adaptational mechanisms (e.g. Hood, 1978; Hood et al., 1978) is that the half-saturation constant of the H-function is not fixed but rather corresponds to the prevailing illumination level. By this mechanism, which is equivalent to a shift of the H-function along the intensity axis, a high sensitivity of the visual system for intensity differences, and thus for contrast, can be maintained throughout the tremendously large range of possible illuminations. The smaller the difference between the value of the half-saturation constant and the pattern-average luminance, the smaller will be the deviation from a logarithmic prediction. The deviations found for higher pattern-average luminances are smaller than would be expected if the half-saturation constant were fixed around 0.25 cd/m^2 (especially for the 0.7 contrast condition). This agrees well with the notion of a shift of the H-function along the intensity axis. However, the negative deviation values found for these higher pattern-average luminances point toward half-saturation constants that are still lower than the pattern-average luminance (if both values were identical, deviations near 0% would be expected). In other words, the shift of the H-function is obviously lagging behind the prevailing average luminance.

The converse is probably true for the lower half of the pattern-average luminances tested: Here the H-function could presumably not shift further down the intensity axis because it reached its dark adapted state. It is quite reasonable, therefore, to assume that the value of the half-saturation constant will be fixed under these low luminance conditions (e.g. Valeton and Norren, 1983). Consequently the pattern-average luminances will always be below the value of the half-saturation constant and the deviation values will be expected to become more positive with decreasing pattern average luminance. Because of the fixed half-saturation constant, the deviation data

obtained in this luminance region are more likely to be a result of the shape of the underlying transducer function. This is the reason why these data were mainly selected for the optimum fit procedure.

There still remains the question of how the deviation data obtained under red-light conditions can be related to a cone-rod transition at a pattern-average luminance of about 0.1 cd/m^2 . Concerning this, there are two things worth noting. Firstly, the large positive deviation values found at this average luminance indicate that the pattern was processed with the lower tail of a hypothetical H-function. In this particular region of the transducer-function, the visual system will be less sensitive to differences in intensity and therefore to contrast. Hence under these suboptimal conditions for the cone system it is likely that the rod system will take over the processing of the plaid pattern. Second, the return to smaller deviation values at very low pattern-average luminances, probably caused by rod intrusion, is another indication that the cone system has reached its lower sensitivity limit.

3.2.3 Contrast Thresholds

Fortunately the experimental method used allows an independent test of the above lines of reasoning. The inability of the cone system to process plaid patterns with pattern-average luminances below 0.1 must necessarily be paralleled by a dramatic increase in the contrast thresholds for the checkerboard fundamental Fourier components. That this is true is demonstrated in *Figs. 18a* (F.H) and *18b* (M.M.); in which the calculated contrast thresholds for the checkerboard fundamental components have been plotted against the pattern-average luminance (filled circles). For comparison the contrast thresholds obtained under white-light conditions with pattern contrasts of 0.5 and 0.7 have been included (open squares). For pattern-average luminances above 0.5 cd/m^2 ($-0.3 \log \text{ cd/m}^2$), the contrast thresholds for the red-light condition are comparable to those of the white-light condition. An almost exponential increase of contrast thresholds can be observed for the red-light thresholds below that value, whereas the white-light contrast thresholds increase only moderately and seem to reach a plateau. The contrast thresholds for the 0.5 and the 0.7 pattern contrast

conditions are very similar, except that there appears to be an upward shift for the higher pattern contrast.

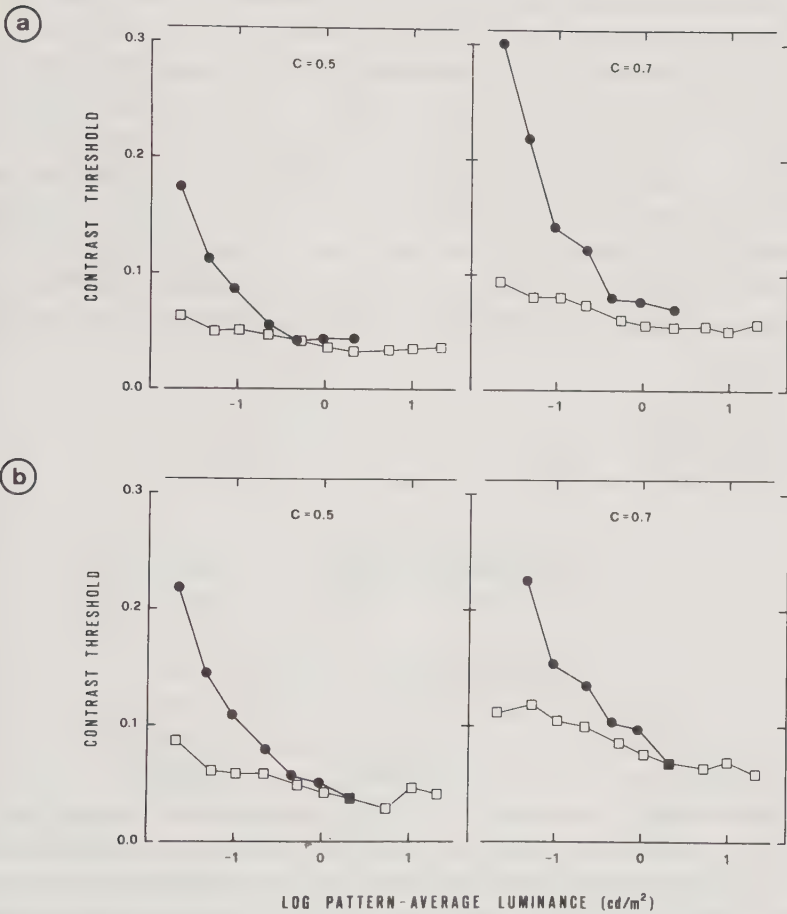


Fig. 18: The contrast thresholds for the checkerboard fundamental components for subjects F.H. (a) and M.M. (b).

The filled circles (●) are the data obtained under red-light conditions. Two pattern contrast conditions (0.5 and 0.7) are shown. For comparison the corresponding white-light data (□) are added to the figures.

From the following assumptions, the contrast threshold data for the red-light condition can be predicted by a H-function:

The slope of the H-function at a specific point determines the visual systems sensitivity to contrast. For example, the difference of two intensities (contrast) has to be much higher at the lower tail of the H-function in order to elicit the same difference in response as in the central part of the function (see *Fig.15*). In the log domain the maximum slope of the H-function is located at the half-saturation point and is monotonically decreasing for values above and below that point. Since contrast can be regarded as the ratio of two luminance values, which is equivalent to the log difference of the luminance values, the slope values have been calculated according to the log derivative of the H-function. *Equation 9a* below is the log domain H-function and *Equation 9b*, the log domain first derivative of that function.

$$H(I) = \frac{10^{n \cdot I}}{10^{n \cdot I} + 10^{n \cdot \sigma}} \quad (9a)$$

$$H'(I) = \frac{\ln 10 \cdot n \cdot 10^{n \cdot I} \cdot 10^{n \cdot \sigma}}{(10^{n \cdot I} + 10^{n \cdot \sigma})^2} \quad (9b)$$

$$T(I) = H'(I)^{-1} \cdot k \quad (9c)$$

I is the log-intensity (luminance), σ the log half-saturation constant and n an exponent. *Equation 9b*, therefore, describes the relative contrast sensitivity for different intensities which can be expected according to an H-function. The hypothetical contrast thresholds (T) are now equal to the inverse of the slope times a proportionality constant k (*Equation 9c*). *Fig.19a* (F.H.) and *19b* (M.M.) show the optimally fitting hypothetical contrast threshold functions based on the H-function derivative. The parameter which has been optimized was the proportionality constant (k). The exponent (n) and the value for the half-saturation constant have been taken from the simulation of the deviation data described in the previous section. Only the data indicated by a horizontal dash have been entered into the optimization procedure.

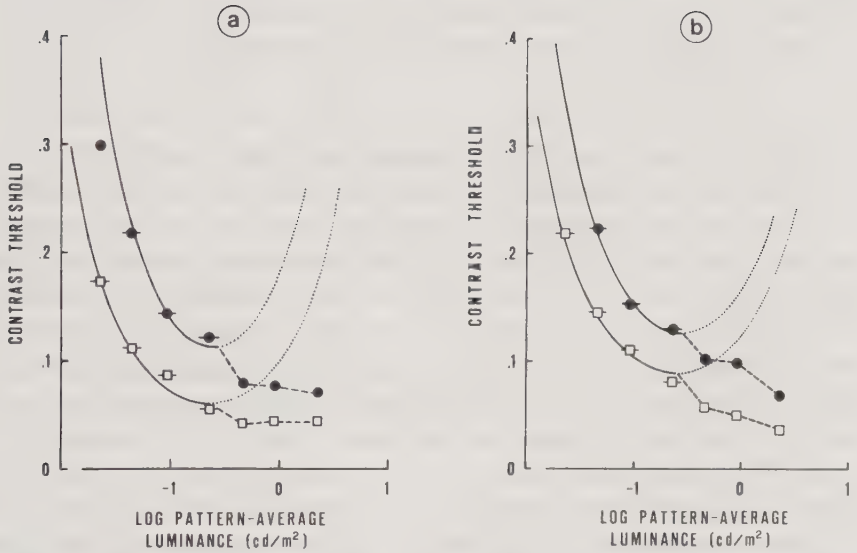


Fig. 19: The best fitting contrast threshold functions according to the H-function derivative.

The solid lines are the fitted functions up to the half-saturation point of the hypothetical H-function. Beyond this point the fitted functions are drawn as stippled lines, and the data are connected by dashed lines. The plots show the data for subjects F.H. (a) and M.M. (b) and for pattern contrasts of 0.5 ($\square$) and 0.7 ($\bullet$).

For pattern-average luminances below the half-saturation points, the simulated contrast threshold curves match very well the experimental data. With fixed half-saturation constants the contrast thresholds should go up again for pattern-average luminances above the values of these constants (dashed curves). This is obviously not the case because with increasing pattern-average luminance the contrast thresholds decrease in a step-like manner and then remain fairly constant (at least for subject F.H.). The fact that the contrast thresholds remain almost constant at higher pattern-average luminances can be well explained by a shift of the H-function along the

intensity axis due to adaptational mechanisms. However, it still remains unclear why there is a step-like decrease in the contrast threshold data at a pattern-average luminance of about $-0.5 \log \text{ cd/m}^2$.

In general, the contrast threshold data for the red-light condition corroborate the hypothesis that there is a transition from predominantly cone to rod mediated vision at pattern-average luminances around 0.1 cd/m^2 . It seems that the bias toward the cone system, caused by long-wavelength stimulation, produces a rapid decline of the visual system's sensitivity to contrast at lower pattern-average luminances. With broadband wavelength stimulation, the rod system takes over the processing of the pattern such that, even for the lowest pattern-average luminances tested, the loss in sensitivity is only marginal. The contrast threshold data as well as the deviation data can be modelled consistently with an H-function as the underlying transducer function.

Finally, the discontinuity (dip) observed in the white-light deviation data at a pattern-average luminance of about 0.1 cd/m^2 is most likely related to a transition from cone to rod mediated vision. The question why this discontinuity is peak-shaped for subject M.M. will be left to the General Discussion section.

Chapter IV

GENERAL DISCUSSION

4.1 The Transducer-Function

4.1.1 Psychophysical Evidence for a H-Function

In contrast to neurophysiology methods, psychophysical ones do not allow a direct measurement of the transducer function for luminance in terms of response amplitudes. Perhaps the closest psychophysical approach to an response amplitude measurement is the method of brightness magnitude estimation developed by S.S. Stevens (1958). Unfortunately this approach suffers from serious problems, such as the relatively low accuracy and huge variation in the observer's judgment of sensation with different experimental parameters (Poulton, 1968). Moreover, the validity of inferring a transducer function from magnitude estimation measurements strongly depends on the assumption that the subjective scaling process is linear. MacKay (1963) has pointed out that if both transduction and subjective scaling follow a logarithmic function, the power law, which Stevens observed, would indeed be expected. Thus one must be wary of directly applying Stevens's findings to the sensory transducer stage.

An indirect derivation of the visual system's photo-transducer properties can be obtained by measuring increment thresholds on background fields differing in spatial and temporal extent. Despite the fact that some investigators derive power-law response compression from such measurements (Mansfield, 1976; Thijssen and Vendrik, 1971), there is a huge bulk of evidence in favour of the S-shaped transducer function (H-function) given in

Equation 6 (Alpern, Rushton and Torii, 1970a, 1970b; Hood, 1978, Hood et al. 1978; Geissler, 1978, 1981, 1983; Adelson, 1982). There is also general agreement that light adaptation can be best understood by assuming that a multiplicative adaptation process precedes the non-linear transduction stage. In physical terms, such a mechanism is identical to introducing a neutral density filter in front of the eye (dark glass hypothesis). In terms of the H-function, it is identical to shifting the function along the intensity axis or (equivalently) to changing the half-saturation constant. Although pigment depletion is a possible mechanism for adaptation, because it reduces the quantum catch in proportion to the incident light, there is a lot of evidence that faster neural or field adaptation mechanisms must be involved too. According to a model proposed by Hood et al. (1978) for the cone system, adaptational shifts in the H-function occur at intensities far below the values where photochemical pigment depletion becomes effective. Thus, in the cone system, pigment depletion can be mainly considered a mechanism for preventing saturation of the response at rather high levels of illumination.

This stands in contrast to the rod system, which already begins to saturate at intensities where pigment depletion can be neglected (Aguilar and Stiles, 1954). There is still a controversy if the rod system has adaptational mechanisms at all (Dowling, 1967; Penn and Hagins, 1972; compare Adelson, 1977, 1982).

Using a special increment threshold technique Hood et al. (1978) were able to demonstrate that the cone system can also be made to saturate. They presented a 500ms flash on a steady adaptation field. During the flash interval, they delivered a 10ms probing flash. The increment threshold for the shorter probing flash was then determined as a function of the 500ms flash's intensity. They found that the increment threshold for the 10ms flash obeyed Weber's law at low and moderate intensities of the 500ms flash, indicating a logarithmic transducer function. But at higher intensities the threshold for the probing flash became infinitely large, suggesting a saturation of the cone systems response. The most interesting finding of their study was that changing the steady field intensity changed the saturation intensity for the probing flash. This finding is consistent with the notion that adaptation shifts the H-function along the intensity axis.

However, the data of Hood et al. are not consistent with the idea that the H-function is always centered on the adapting field's intensity. Such a range control mechanism is logically required if the visual system's sensitivity is to be maintained over a dynamic range of intensities exceeding that of the H-function. For such exigencies an increase in the adapting field intensity should be paralleled by an increase of the half-saturation constant by the same amount. Instead, Hood et al. found that the increment for the half-saturation constant is much less than would be expected on a one to one basis, for adapting field intensities below 4 log trolands. At higher adapting field intensities, however, they found a one to one relationship.

A particular problem with Hood et al.'s findings is that, at the dimmest adaptation field tested (1.3 log trolands), cone saturation occurs at an intensity more than 3 log units away. Since the dynamic range of the H-function is only about ± 1.5 log units this implies that the 1.3 log troland adaptation field was being processed within the lower tail of the H-function. This does not make any sense because it entails that the visual system is much more sensitive to intensity increments than to decrements.

However, a possible way out of this dilemma is to reject the assumption that the 500ms flash itself did not push the H-function toward higher intensities. If rather it is assumed that the H-function rapidly shifts during the flash interval, then an apparent outward shift of the saturation intensity would be expected. This may explain the large differences in adaptation field and saturation intensity found at moderate adaptation field intensities (see above).

Support for this hypothesis comes from the physiological data of Shevell (1977). He found that a background flash of 250ms duration, preceding a test flash, caused adaptational effects on the order of 1 to 1.5 log units.

Yet, Hood et al.'s data measured for higher adapting field intensities nicely fit a model based on a H-function, centered on the ambient intensity. Here, not only the point of saturation shifts by the same amount as the adapting field intensity does, but also the log difference between these values is around 1.2 log units. Since the H-function saturates about 1.5 log units away from its center, this is exactly what one would expect if the H-function was centered at the adaptation field intensity. There still remains the question, nevertheless, why only the data measured with high intensity adapting fields match this model? A possible explanation is that at

higher intensities the flash does not push the H-function to the right because pigment depletion, with its slower time course, and not neural reorganization, is the main adaptational mechanism.

Despite the problems stated above, the findings of Hood et al. support the hypothesis that the transducer properties of the cone system can be described by an H-function whose half-saturation constant changes with the ambient level of illumination.

In the present investigation the same hypothesis turned out to be an adequate description of the characteristics of the transducer function at its lower end (red-light data). Thus my findings taken together with those of Hood et al., which complement the picture for the upper end of the transducer function, suggests that the H-function is a very powerful working model.

4.1.2 The Half-Saturation Constant

With a fixed half-saturation constant, the H-function has a dynamic range of only about ± 1.5 log units. For a reasonable resolution of intensity differences, and hence for contrast, this range will be even less than ± 1 log unit. A possible way for the visual system to maintain its sensitivity over the enormous variation of naturally occurring illuminations is the range control mechanism described above.

The dramatic effects that occur under conditions where the visual system is obviously unable to adjust the half-saturation constant are demonstrated in the red-light experiment. At very dim illuminances there is presumably a point where the half-saturation constant will retain a fixed value, regardless of how low the illumination is. As a consequence the difference in response for two intensities (contrast) shifted down the intensity scale will decrease dramatically. This is because the H-function asymptotes with the intensity axis at its lower tail (compare *Fig.15*) and the difference in response will virtually be zero in this region. The steep increase in the contrast thresholds observed in the red-light data is perfectly consistent with the hypothetical behaviour of an H-function having a fixed half-saturation constant (see *Fig.19*). In addition, the deviations from a logarithmic pro-

cessing observed at lower luminances (red-light data) also match the hypothetical characteristics of an H-function. The notion that there is a fixed 'dark adapted' value for the half-saturation constant is corroborated by many neurophysiological investigations of the response behavior of receptors and retinal neurons (e.g. Boynton and Whitten, 1970; Werblin, 1974; Valetton and Norren, 1983).

Nevertheless, there is considerable evidence that, when the ambient illumination is increasing from low to moderate intensities, the half-saturation constant follows the shift. For, if the half-saturation constants in the present study remained fixed, then the deviations from a logarithmic processing should increase towards large negative values with increasing illumination levels (compare *Fig.17*). This, however, is not the case for the white-light, nor for the red-light, data. Instead, the deviations first slide down to moderate negative values and then, above pattern-average luminances of 2 cd/m², remain fairly constant (see *Fig.9a-c*). Such behavior can only be explained if the half-saturation constant of the H-function is allowed to change. To maintain constant deviation values with increasing pattern-average luminance an even stronger assumption must be made: namely, the H-function must shift by exactly the same amount (factor) as the pattern-average luminance is increased.

For every pair of luminance values (black and white squares) the luminance that gives a response half-way in between (grey squares) is uniquely defined by the relative position of the H-function on the intensity axis. The hypothetical value for the half-saturation constant (σ) can be calculated on the basis of the experimental data from the following equation:

$$\sigma = \left[\frac{g^n (b^n + w^n) - 2b^n w^n}{b^n + w^n - 2g^n} \right]^{1/n} \quad (10)$$

where b and w are the luminances of the black and white squares, g the geometric mean of the upper and lower threshold luminance for the grey squares and n an exponent. It is easy to see that multiplying the b , w

and g values by a constant factor will change the half-saturation constant by the same factor. In other words, if with an increase in pattern-average luminance, the g value retains its relative ratio with respect to the b and g values (which is equivalent to a constant deviation from a logarithmic prediction) the half-saturation constant must increase by the same factor as the pattern-average luminance.

Yet the negative, although constant, deviation values above 2.2 cd/m^2 (white-light data) indicate that the H-function is not centered exactly at the ambient illumination level. In this luminance range and for pattern contrasts above 0.5 all three subjects show an almost constant log offset between pattern-average luminance and calculated half-saturation constants. The center of the H-function appears to be located around 0.3 log units (a factor of two) below the respective pattern-average luminance. A problem with this comparison is that the pattern-average luminance is an arithmetic mean representation. For the quasi-logarithmic H-function, however, a geometric mean representation would be more appropriate. But even when the calculated half-saturation constants are compared to the geometric mean luminance of the plaid pattern their values are still lower. In *Fig.20* this is demonstrated by plotting the log differences between half-saturation constant values and pattern-average luminance as a function of pattern contrast. The log differences shown represent the grand mean across all subjects and pattern-average luminances between 5.5 and 22 cd/m^2 . The data for pattern contrasts below 0.5 have not been included in the plot because they were too noisy. Since at lower contrasts small differences in the deviation values have large effects on the value of the half-saturation constant a larger scatter is to be expected. The filled circles in *Fig.20* represent the log difference between the pattern *arithmetic* mean luminance and the calculated half-saturation constants. Although all log difference values are close to a value of about -0.3 , there is a slight tendency for them to be smaller with increasing pattern contrast. This tendency is much more pronounced when the log difference is calculated on the basis of a pattern *geometric* mean luminance (filled squares).

Nevertheless, as demonstrated in *Fig.20*, even for the geometric mean comparison, the log difference never reaches zero. Why does the visual system display such a behavior, which in terms of an automatic range control mechanism would be suboptimal?

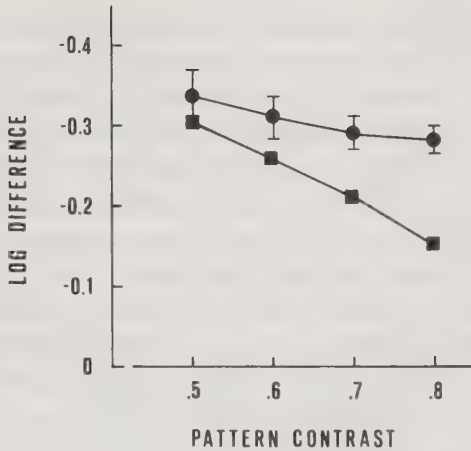


Fig. 20: Log differences between the half-saturation constants and the pattern-average luminance as a function of pattern contrast. The filled circles (●) represent the log differences obtained by calculating the arithmetic mean luminance of the plaid pattern; the filled squares (■), those obtained by calculating the geometric mean.

A plausible explanation is that the artificial laboratory conditions under which the experiment was conducted were very different from natural settings. A pattern, although relatively large in extent (11°), put in the middle of a sea of darkness is in fact not a good simulation of naturally occurring scenes. There is considerable physiological evidence that the response properties of receptors and neurons in the retina can be altered by background stimulation very distant from the site of recording (e.g.: Werblin, 1974; Werblin and Copenhagen, 1974; Thibos and Werblin, 1978; Steinberg, 1969; Marchiafava, 1983; Valberg et al., 1985). It therefore is conceivable that adaptive processes are not spatially confined to the extent of the receptors stimulated, but involve some sort of averaging across large parts of the visual field. Thus the dark surround of the pattern could have been responsible for the half-saturation constants falling short of the pattern-average luminance.

The sensitivity control process in the visual system is probably confronted with the same problems that engineers face when they develop an automatic exposure meter for a camera. The similar goal is to maintain the resolution of contrast under a variety of illumination conditions. A good strategy is to encompass to some degree the illumination properties of naturally occurring scenes. One particular problem is that in landscape pictures a uniform averaging of intensities will usually lead to underexposures, because of the bright sky covering large parts of the image. This can be avoided by selectively weighting the upper part of the field less than the lower one. With respect to average intensity, the picture would then be overexposed. The advantage of such an exposure strategy resides in the better contrast resolution of details in the landscape. For biological visual systems the same advantage would apply, because relevant information is usually contained in the structure of the landscape and not the sky. Why, therefore, should the visual system not use such an 'overexposure' strategy?

One possible counter-argument is that a *local* regulation of luminance gain renders such a strategy unnecessary. However, this would imply that the adaptive process has to be extremely fast in order to avoid strong inhomogeneities in sensitivity (e.g. strong afterimages) with eye movements. Since especially dark adaptation is a rather slow process, a more globally operating gain-mechanism is more likely.

The best test for the 'overexposure hypothesis' would be to repeat the afterimage experiment with a plaid pattern surrounded by a large bright field. The values for the half-saturation constants would then be expected to be closer to the pattern-average luminance. Unfortunately technical limitations, resulting from the problem of how to correct the sensors for stray light, did not allow the hypothesis to be directly tested.

Instead, the 'overexposure' hypothesis was tested with a different method, which was not quite as elegant as the method mentioned above. The rationale of the experiment was as follows.

After an exposure to a bright field the H-function presumably does not shift immediately back to its previous position, but rather slowly asymptotes to it over time. During this interval the transduction properties will be different with respect to those in the unadapted state. Thus, for the plaid pattern experiment, the luminance of the grey squares giving a response

halfway between those of the black and white squares (no afterimage) will be expected to change too.

Fig.21 shows the results of such an experiment. Before each adaptation sequence the subject (F.H.) was exposed for a period of 20 seconds to a bright, uniform, adaptation field. The luminance of the adaptation field was 300 cd/m² and 1500 cd/m², the pattern-average luminance was 5.5 cd/m² (white tungsten light) and the pattern contrast was 0.7.

In order to avoid a contamination of the data by pupillary action a delay of five seconds was interposed between the pre-adaptation and the onset of the pattern. In this interval, the pupil had enough time to revert to its static value of about 4mm (cf., Wysecki and Stiles, 1982).

The data in *Fig.21* are again expressed in terms of the percent deviation of the grey squares from the geometric mean of the black and white squares at the upper and lower threshold for the presence of the afterimage. The white and shaded bars represent the deviations at the upper and lower thresholds, respectively. Standard deviations are plotted at the end of each bar. The horizontal line, bisecting the bars, is the geometric mean of the upper and lower threshold deviations. The two pre-adaptation conditions and a control (no pre-adaptation) are indicated above each bar plot. The deviation values clearly demonstrate that the asymmetry between upper and lower thresholds, observed in the control condition, decreases with pre-adaptation to a bright, uniform, field. For the 300 cd/m² field, the mean deviation reduces to 5%; for the 1500 cd/m² field it reduces to almost 0%. In terms of the H-function hypothesis, this suggests that the half-saturation constant is then very close to the geometric mean luminance of the plaid pattern.

The hypothesis that the H-function is shifted to the right with respect to the control condition is supported by the decrease in distance between the upper and lower threshold values. A calculation of the contrast thresholds for the checkerboard fundamental components reveals that they are around 12% lower for the pre-adapted conditions. This is on the order of magnitude of the theoretical improvement (7%) predicted from the H-function derivative (*Equation 9*).

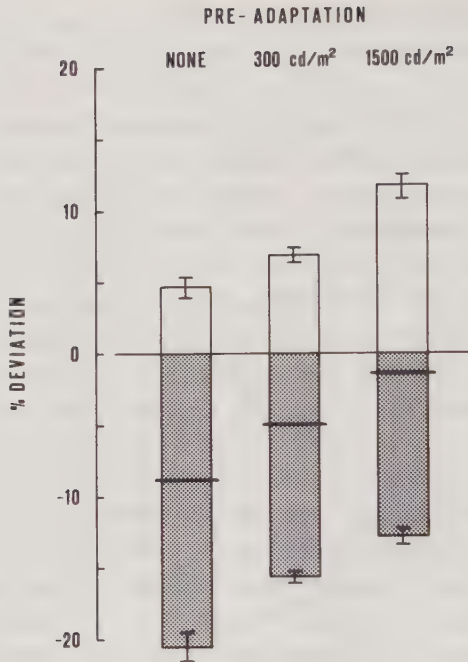


Fig. 21: Deviations from a logarithmic prediction following pre-adaptation to a bright background field

What can be concluded from this pre-adaptation experiment? First of all it provides evidence for the hypothesis that the moderate negative mean deviation values found for the unadapted case (control) are due to a H-function whose center is located below the pattern-average (arithmetic or geometric) luminance. Second, the increase in contrast sensitivity with pre-adaptation shows that the visual system was indeed suboptimally tuned to the plaid pattern in the control condition. It therefore is reasonable to assume that under more natural conditions, where the distribution of intensities is not quite as artificial as in laboratory situations, the system will perform more adequately.

It is of some interest to consider the neurophysiological evidence for a half-saturation constant falling short of the ambient luminance. Boynton and

Whitten (1970) have recorded the late receptor potentials in monkey cones under different levels of ambient illumination. Their results not only show the characteristics of a H-function shifting along the intensity axis, but also indicate that at moderate to high background illumination levels the dynamic range of the response functions is biased towards lower intensities. This is exactly what one would expect if the H-function is centered below the background illumination level.

Jacobs (1965) investigated the effects of light adaptation in the lateral geniculate nucleus (LGN) of the squirrel monkey and found a similar result: At very low background illuminations the cells showed a higher gain for luminance increments. The reverse was true for moderate background illuminations, where the cells were more sensitive to luminance decrements. This behavior can be well explained by the H-function model. At very low intensities the H-function is locked at its 'dark adapted' position (compare the red-light data) and consequently for any background intensity falling below this value, the gain will be higher for increments than for decrements. On the other hand, at moderate background intensities where the H-function is centered at lower intensities ('overexposure' hypothesis) a response bias towards decrements is to be expected. Another finding of Jacobs (1965) is that the entire dynamic response range does not exceed the adaptation luminance by much more than plus or minus one log unit. This is very close to the theoretical dynamic range given by a H-function.

4.1.3 The Cone-Rod Transition

The cone-rod duplexity of the human retina represents more than a mere range switch. There are also vast qualitative changes introduced with the transition from photopic to scotopic vision. Rod mediated vision gains its high sensitivity to light at the expense of spatio-temporal resolution and color discrimination. Under scotopic illumination conditions the central fovea is almost scotomized because it mainly contains cones.

The reason why the visual system gives up these otherwise useful features is probably due to the quantal nature of light. Quantal noise increases dramatically at very low illumination levels. There are two possible ways to cope with this physical constraint. The first is to integrate the incoming quanta over a larger area and thereby increase the probability of a hit

while stabilizing the response. Here the solution is to increase spatial integration in the retina at the expense of spatial resolution. The second way is to increase the integration time (exposure). This will also reduce quantal noise, but at the expense of slowing the system down. In the human visual system, the spatial pooling (convergence) of rod signals and the increased integration times (decrease in CFF) is a compromise between these two noise reduction mechanisms.

The present investigation was less concerned with the spatio-temporal changes at the transition from photopic to scotopic illumination, as with the changes in the transduction characteristics. The red-light experiment demonstrates that cone vision can only adequately process the plaid pattern down to pattern-average luminances of about 0.25 (-0.6 log) cd/m^2 . This value is, of course, not equivalent to the absolute threshold of the cones, because the H-function will still give a response below this point. However, a rough estimation of the absolute cone threshold can be made by the following assumptions:

The absolute contrast threshold for a sine-wave grating of 1.2 c/deg (spatial frequency of the afterimage components) at a luminance of 0.25 cd/m^2 is about 0.005 (van Meeteren and Voss, 1972). Now let the center of the H-function be fixed at this luminance. The difference in the H-function output for two luminance values located around its center and having a contrast of 0.005 will be 0.0025. For the sake of simplicity let's assume that this value will be the threshold necessary to detect a difference in luminance throughout the entire range of the H-function. Now it is very simple to calculate the minimum luminance at which the H-function reaches the threshold value of 0.0025. Interestingly, this luminance turns out to be $6 \cdot 10^{-4}$ (-3.2 log cd/m^2), almost exactly the value for the absolute cone threshold (around -3.5 log cd/m^2 , from Hood and Finkelstein, 1986; around -3.0 log cd/m^2 , from Le Grand, 1957). The consistency of this hypothetical value with absolute threshold measurements strongly suggests that 0.25 cd/m^2 is the lowest possible value for the half-saturation constant of the cone H-function. Because cone mediated vision will deteriorate for luminances below this value the rod system must take over the processing in order to maintain visual sensitivity. A comparison of the contrast thresholds obtained under red-light (cones) and white-light (cones and rods) conditions in the present investigation provides a striking example for the maintenance of sensitivity in the duplex retina (see *Fig.18*).

For the red-light condition, the changes of transduction properties with decreasing luminance have already been discussed extensively in section 3.2. There remains the question, however, of what evidence the white-light data provides for the transition from predominantly cone to rod mediated vision. Generally this change in the receptor system is indicated by two phenomena: First of all, below 2 (0.3 log) cd/m^2 the mean deviation from a logarithmic prediction gets progressively smaller with decreasing pattern-average luminance. At about 0.2 (-0.7 log) cd/m^2 the deviation data reach a first minimum (see *Fig.9a* and *b*).

This behavior can be well explained by an H-function that cannot shift further to the left because it is slowly reaching its dark adapted limit. In other words, when, at moderate pattern intensities, the half-saturation constant was always located below the pattern-average luminance, this difference will decrease by lowering the intensity. A minimum in deviation from a logarithmic prediction should then occur when the pattern-average luminance coincides with the dark adapted value of the half-saturation constant, because for this condition the H-function has nearly perfect logarithmic transducer properties. From the red-light experiment we know this value for the cones to be around 0.25 (-0.6 log) cd/m^2 , just about the point where the white-light deviation data show their first minimum.

However, for the remaining lower-intensity part of the white-light data, the cone transducer function cannot provide an explanatory basis. Here we find that, after a short return to larger negative deviations (dip), the deviation values reach a second minimum (compare *Fig.9a* and *b*, subjects S.R. and F.H). The cone H-function would have predicted a large increase toward positive deviations, just as is found under red-light conditions. The return to larger negative deviation values in the white light data can only be explained if a different transducer function, namely that of the rods, comes into play. As has been mentioned already before, the transducer function of the rods is also considered to be an H-function, but with a half-saturation constant located below that of the dark adapted cones (for psychophysics see Walraven and Valeton, 1984 (fit of the data of Aguilar and Stiles, 1954) and Adelson, 1982; for physiology see Fain and Dowling, 1973; Fain, 1976). The return to larger negative deviations (white light data) at around 0.1 cd/m^2 might then be explained by the influence of the rod transducer function which, because of its center being located below the pattern-average

luminance, will produce negative deviations. Consequently, as the pattern-average luminance is lowered further, the distance to the rod H-function center will be reduced and the deviation values will be expected to become smaller. Despite its consistency with the deviation data, the above explanation remains only a tentative one.

There are a lot of open questions which cannot be answered satisfactorily by the given data. For example, it is still unclear to what extent the remaining cone signals will have an influence on the deviation data for pattern-average luminances below 0.25 cd/m^2 . For this reason it is impossible to make any quantitative assessments about where to locate the rod H-function center at the three lowest luminances tested.

A second line of evidence in support for the cone-rod transition hypothesis is given by the data of subject M.M.. In the area of interest (i.e. low luminances) they reveal quite a different behavior. As has already been pointed out, the deviation data of subject M.M. have a great similarity with the characteristics obtained under red-light stimulation. To be more specific, at 0.1 cd/m^2 the data of M.M. show a peak of positive deviations whereas the data of the other subjects show a dip-like return to larger negative deviation values (see *Fig.9*). There are two possible explanations for this difference. First, in subject M.M. the sensitivity of the rods is so reduced that, even at low luminances, the plaid pattern is predominantly being processed by the cone system. If this is so, then it is not surprising that the white-light deviation data resemble those of the red-light experiment. A second possibility is that the center of the rod H-function is markedly lower than in the other two subjects, such that there is a gap in the transition from cone to rod mediated vision. This, however, implies that subject M.M. should be more sensitive at very low intensities, because the range of his H-function extends further down.

A clarification of the issue comes from a dark adaptation curve measured with a Goldman-Weekers adaptometer (University hospital Zürich, courtesy of Prof. Niemeyer). As can be seen in *Fig.22* the fully dark adapted threshold for subject M.M.'s rods is located at the upper limit of the normal range (shaded area). Although M.M.'s elevated threshold is not considered pathological, it tends to support the reduced rod sensitivity hypothesis.

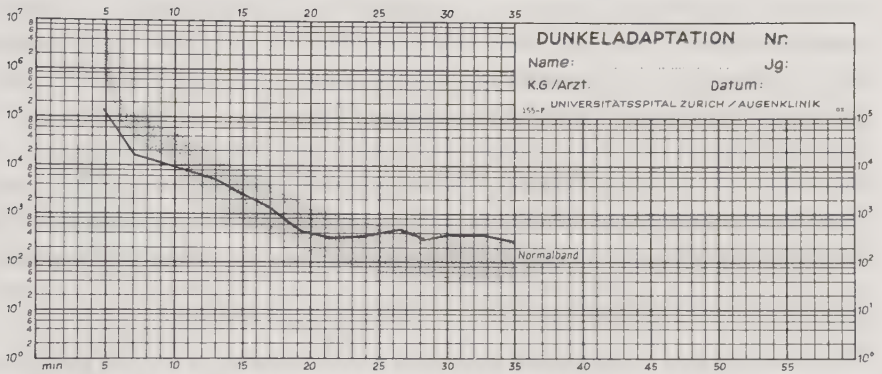


Fig. 22: Dark adaptation curve for subject M.M.

Additional evidence for this hypothesis is given by the contrast threshold values of the white-light experiments. Subject M.M. shows a much steeper increase in contrast threshold with decreasing pattern-average luminance than the other two subjects (Fig. 11a-c). This is to be expected, if M.M. has a reduced rod sensitivity. It, therefore, seems not too far-fetched to consider reduced rod sensitivity as the underlying cause of M.M.'s anomalous data.

To conclude, there is much evidence in favor of the hypothesis that a transition from predominantly cone to rod mediated vision occurred at a luminance of about 0.1 cd/m^2 .

4.1.4 Theoretical Advantages of a H-Function

The quasi-logarithmic transduction properties of the H-function have an advantage that has not been mentioned yet. One of the basic requirements for object constancy is that objects look the same even with changes in the ambient level of illumination. The physical dimension that discards the illuminant is contrast. This arises from the fact that the ratio between reflecting surfaces does not change with the strength of the illuminant. There is

a lot of evidence that the visual system is able to maintain this contrast constancy over a wide range of illuminations (e.g. Kulikowski, 1976). In order to physiologically represent contrast, the visual system must somehow calculate the ratio of different intensities falling onto the retina. Given a logarithmic transducer function the problem reduces to a simple subtractive operation. Since in neural terms subtraction can easily be handled by an integration of excitatory and inhibitory inputs, a logarithmic or quasi-logarithmic pre-processing of intensity seems to be the most parsimonious (Cornsweet (1970) has argued along similar lines to explain hue perception).

The question then arises, why in the visual system is the representation of contrast complicated by using a range adjustable H-function rather than a plain logarithmic transducer function. If, however, one takes into account the constraints of neural information processing, then there are indeed several arguments in favour of the H-function.

One particular problem is that with respect to their intrinsic noise, the response range of neurones is relatively small. This implies that the larger the intensity range covered by a sensory transducer, the poorer its resolution. If, for example, the cones were plain logarithmic transducers, coding intensity monotonically over the entire photopic range, then the resolution of intensity differences, and thus contrast, would be unacceptably poor. The fact, however, that in natural scenes the differences in intensity seldom exceed a factor of 200 (a contrast of 0.99) entails that a single transducer function, covering the entire intensity range, is an unnecessary waste of sensitivity. The optimal solution to this problem is to discard the unwanted mean illumination level (DC-signal) and to process only the limited range of intensity differences around it (AC-signal). A range adjustable H-function has exactly this property. Such a function provides, therefore, not only a basis for logarithmic transduction but also a high level of sensitivity throughout the entire range of illuminations.

The common purpose of the different range control mechanisms (neural adaptation, pigment depletion, pupillary action) can thus be considered as means for reducing the efficiency of the incoming light and thereby as a way of normalizing the response. An interesting consequence of this is the

implication that the Weber-Fechner law, which can be observed over a wide range of intensities (rods and cones), is not due to logarithmic processing but rather to the range control mechanism. A simple example will demonstrate this.

Let us assume that the response to a stimulus with an intensity of one is unity and that the incremental threshold associated with it is 0.1. If a stimulus with an intensity of 100 is then presented, the range control mechanism of the system will reduce the efficiency of that stimulus by a factor of 0.01. Thus, the output of the system will be unity too. To reach the incremental threshold in this case, a test stimulus has to have an intensity of 110. This is just what Weber's law predicts. The interesting point, however, is that the threshold did not increase in proportion to the stimulus intensity because of a logarithmic transducer function and a constant threshold criterion on the response side. Rather, it is the normalizing mechanism that is responsible for Weber's law. The actual form of the underlying transducer function does not matter because a linear, compressive or even accelerating relationship between intensity and response would produce a similar result. The only way to distinguish between these different transduction alternatives is to measure where the visual system locates an intensity midway between two other intensities, as was done in the present investigation.

Another advantage of the H-function is its particular shape. Grossberg (1973, 1983) has demonstrated that a sigmoid response function is ideal for suppressing signal noise and for enhancing contrast as well as for normalizing suprathreshold activities. The suppression of noise is due to the lower accelerating part of the sigmoid, which increases the signal to noise ratio. The middle part and the compressive upper section are responsible for the other properties listed above.

4.2 The Afterimage Method

4.2.1 Bisection Techniques

The afterimage method used in the present investigation can be regarded as a bisection technique. In this sense it is similar to a method used by Plateau (1872) more than a century ago. Plateau gave a pair of painted black and white disks to eight artists and asked them to paint a grey disk midway between them. The resulting grey disks were nearly identical for all eight artists, in spite of the different illumination conditions under which they were produced. This provided a nice qualitative demonstration of contrast constancy. Since Plateau's original experiment, many other quantitative assessments of lightness scales have been based on the bisection techniques. The results of these experiments are usually well described by power-functions, which can be linearly related to the functions obtained by magnitude estimation (Bodmann et al., 1980).

A major difference between the bisection technique and the afterimage method used in these experiments is that the grey midway between black and white is not determined by estimating it. Instead, it is inferred from a measurement of thresholds, which do not involve subjective scaling of the stimulus. Thus, the results of the afterimage experiments most likely reflect the mere sensory stage characteristics rather than the combined properties of sensory transduction and subjective scaling. Because the two approaches are different, the quasi-logarithmic processing of luminance found in the present study does not necessarily cross with the power function relationship observed in bisection or magnitude estimation experiments.

4.2.2 Possible Mechanisms

When considering which mechanisms are responsible for the plaid pattern afterimage effect, an obvious question comes to mind: Is the effect retinal or cortical in origin? This question is important because the level in the visual pathway mediating the effect predetermines which structures and mechanisms can be invoked to explain it.

The literature on afterimage effects and their hypothetical neural or photochemical correlates is enormous (for a review, see Brown, 1965). The present afterimage effect differs from most of the studies published in that it rules out pigment depletion or strong local adaptational changes as an explanation. (This follows from the fact that, even for the highest luminances tested, only negligible amounts of pigment were bleached.)

Nevertheless, there are a few reports of afterimages generated with low intensity stimuli, which also invoke neural factors as being the origin (e.g. Mariotte, 1965; Koenderink, 1972). Among these, one is particularly relevant to the afterimage effect reported here.

Virsu and Laurinen (1977) used counterphase-modulated sinusoidal gratings to generate strong afterimages whose spatial frequency was double that of the input grating. Their experiment is very similar to the present investigation not only because it involved counterphase adaptation, but also because it is compatible with an explanation based on a nonlinear luminance transduction in the visual system. The latter point can be clarified in the following way. At high contrasts the bright regions of a sinusoidal grating look broader than the dark ones. If a sine-wave is logarithmically transformed the output will show a similar distortion of the wave-form. The linear addition of two logarithmically transformed sinusoids, shifted in phase by 180° , results in a wave-form having double the frequency. This is because the compressive behavior of a logarithm causes the sum of the peaks and troughs to be less than the sum of the intermediate grey regions. Interestingly, Virsu and Laurinen were also able to fit their data with a H-function, although not quite as successfully as in the present study. Evidence for the neural origin of their afterimage effect comes from an experiment in which the subject was adapted to counterphase modulated sine-wave gratings while his eyes were pressure blinded. After the relief from pressure there was no afterimage present at all. Since it is known that adaptation to bleaching lights leaves the afterimage quite intact (Craig, 1940), pigment depletion can, therefore, be definitely excluded as the cause of the sine-wave afterimages.

Hence it is highly likely that the sine-wave afterimage effects of Virsu and Laurinen and the plaid pattern afterimage effects reported here are being mediated by similar mechanisms.

This can be further elucidated in mathematical terms. When a sine-wave is logarithmically transformed, the Fourier spectrum will contain a strong second harmonic component (double the frequency) in addition to the fundamental component. If the grating is then counterphase modulated, the fundamental component will undergo a phase shift of 180° , whereas the second harmonic will maintain its phase.

A similar situation is given for the plaid pattern experiment; here it is the vertical and horizontal Fourier components of the superimposed square-wave gratings which are adapted in counterphase while the diagonally oriented checkerboard components, introduced by non-linear transduction, will maintain their phase. Thus, the theorem formulated above (see Methods); namely, that the Fourier components adapted in phase will appear in the afterimage, while those adapted in counterphase will cancel, can also be applied to the sine-wave afterimage effect.

Nevertheless such a phenomenological description, no matter how apt, does not provide an explanation of the underlying physiological mechanisms. A tentative attempt at doing so is given below.

Adaptation to a static square-wave grating presumably causes a transient response bias throughout all stages of the visual pathway which is specific for the particular grating (spatial frequency, phase, orientation). Let us assume that, against a neutral background, this bias has its correlate in a negative afterimage. If the same pattern is adapted 180° out of phase with respect to itself, the response bias will be of opposite sign. The specific adaptational effects on the sensitivity of the system will thus cancel. A neutral background will therefore be perceived as a neutral one, which means that no afterimage will be present. In the case of a counterphase adapted plaid pattern the same argument should apply to the superimposed square-wave gratings. However, the potentially present diagonal Fourier components (checkerboard spectrum) will not change their phase during adaptation and will, therefore, produce a response bias that is unbalanced. The overall outcome would then be an afterimage of these components.

The validity of the above hypothesis depends to a large degree on the assumption that the visual system is able to process such diagonal Fourier components. This clearly presupposes the existence of length integrating

mechanisms in the visual system (see Methods). A possible neurophysiological substrate could be the elongated receptive fields of neurones in the primary visual cortex, first described by Hubel and Wiesel (1962, 1968). It is important to note, however, that only the length integrating properties of such neurones are required to explain the present results. Although there is much psychophysical and physiological evidence for spatial frequency selective channels in the visual system (e.g. Campbell and Robson, 1968; Maffei and Fiorentini, 1973), there is no need to invoke such collective properties of neurones to explain the plaid pattern afterimage effect.

4.2.3 A Dichoptic Experiment

Support for the afterimage hypothesis comes from an additional experiment. Instead of being binocularly presented, the two counterphase positions of the pattern were presented to the two eyes separately in an alternating fashion (dichoptic stimulation). This was achieved by means of two electromagnetic shutters placed before the eyes of the subject. The subject was then adapted to the pattern by opening only one shutter at a time. Before the pattern was turned on, a corresponding fixation LED was lit to ensure the subject's correct fixation. After the adaptation period both shutters were simultaneously opened and the subjects task was to detect the presence of a diagonal afterimage grid against a neutral background. In all other respects the dichoptic experiment was the same as in the binocular one. The results of this dichoptic experiment are shown in *Fig.23* (F.H.) for pattern contrasts of 0.2, 0.3 and 0.4 and a pattern-average luminance of 11 cd/m². The result is once again represented as the deviation of the grey squares threshold values (afterimage) from a logarithmic prediction (geometric mean of the black and white squares). As in *Fig.21*, the deviations found for the upper threshold are given by the white bars and those for the lower threshold by the shaded bars. The geometric mean is indicated by the horizontal line. The thin bars represent the data obtained under binocular stimulation.

The first impression is that there is an enormous increase in separation between the upper and lower thresholds for the dichoptic case. Despite this, the mean deviations turn out to be almost identical with those obtained

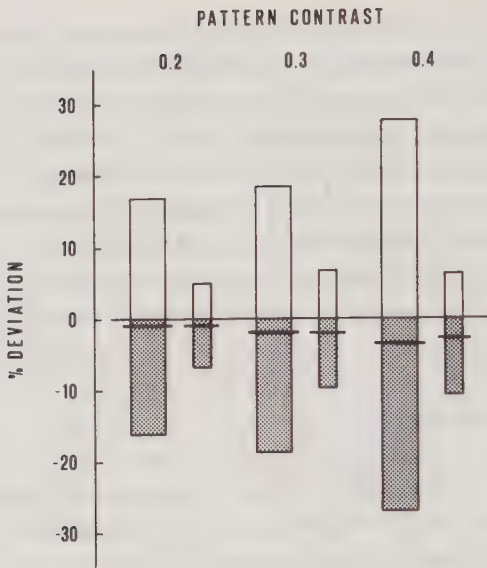


Fig. 23: Deviations from a logarithmic prediction under dichoptic stimulation

in the binocular condition. The most striking result of the dichoptic experiment, however, is that a diagonal afterimage grid could be generated at all. When the neutral background was presented to both eyes there was no afterimage of the horizontal and vertical components of the plaid pattern. Interestingly, with a monocular inspection of the background, an afterimage of these components was present.

There are several conclusions which can be drawn from the fact that the diagonal afterimage grid could be elicited by dichoptic stimulation: First, it suggests that a response bias of opposite sign will cancel even when it is induced in different eyes. Second, it clearly argues for the presence of length integrating mechanisms. This is because, to process the diagonal Fourier components in the dichoptic experiment, the visual system must have integrated at least over the diagonals of two square elements in the plaid pattern. Since the pattern was strictly fixated in the dichoptic experiment, retinal smearing can be definitely ruled out as a factor contributing

to the afterimage. But even in the binocular experiment the movement of the eyes across the pattern can not be considered to have caused artifacts. On the one hand, the afterimage consisted always of two components: one oriented in the same direction as the eye movement and a second oriented in the direction orthogonal to it. On the other hand, counterphase adaptation to the pattern, with eye movements in directions different from the diagonal, did not alter the afterimage, nor the threshold points.

There still remains the question of why in the dichoptic case there is such a large separation between the upper and lower threshold. One possibility is that this decrease in sensitivity is due to the monocular viewing of the pattern. This, however, cannot account for the whole effect. A measurement of the thresholds under monocular counterphase conditions revealed a loss in sensitivity with respect to the binocular condition (factor of 1.5) which was much smaller than the one observed for the dichoptic/binocular case (factor of two and more). Thus, there must be an additional mechanism causing the large increase in sensitivity for the binocular case.

The major difference between the binocular and the dichoptic experiments is that for the latter the pattern phase was fixed with respect to a particular eye. Is it possible, therefore, that the coincident counterphase adaptation of the plaid pattern's *horizontal* and *vertical* square-wave components in the binocular condition, which was absent in the dichoptic condition, caused the sensitivity enhancement for the *diagonal* checkerboard Fourier components? If true, this would clearly imply the existence of orientational interactions. Indeed, the many psychophysical and neurophysiological experiments, demonstrating inhibitory interactions between channels or neurones tuned to different orientations, provides a good basis for accepting this hypothesis (Benevento Creutzfeldt and Kuhnt, 1972; Blakemore and Tobin, 1972; Blakemore, Carpenter and Georgeson, 1970; Carpenter and Blakemore, 1973; Tolhurst and Thompson, 1975; Thomas and Shimamura, 1975; Atkinson, 1972).

According to this hypothesis, in the plaid pattern experiment, the counterphase adaptation of the vertical and horizontal square-wave components will inhibit the channels processing the diagonal Fourier components. When the pattern is subsequently replaced by a neutral background, the 'diagonal

channels' will then be disinhibited. The response bias, introduced by the in-phase adapted diagonal Fourier components could then be enhanced by the disinhibitory response. It is well known that counterphase-modulated stimuli are the most efficient for driving neurones in the primary visual pathway. For example, a simple cell in the visual cortex will respond more vigorously to a counterphase-modulated grating than to a grating being simply turned on and off (identical phase). Furthermore, it can be assumed that in the counterphase condition there are more cells involved in the processing of the grating: one set will be excited by one phase of the grating and another set by the opposite phase. Thus, cells having orientation selectivities different from the grating's, will be more inhibited by counterphase modulated gratings than by gratings presented in a single phase. The higher sensitivity observed for counterphase-adapted plaid patterns could, therefore, be due to larger disinhibition.

Although this hypothesis certainly oversimplifies the matter, it is at least a first approach to identifying the underlying mechanisms of the afterimage effect. Additional evidence in support of this hypothesis comes from another afterimage experiment.

4.2.4 Afterimages from Checkerboards

If, after adaptation to a static checkerboard, a diagonally oriented sine-wave grating is presented for a short time, there will be a strong afterimage resembling the diagonal fundamental Fourier component, oriented 90° to the inducing sine-wave grating. The afterimage will be strongest when the sine-wave grating has the same spatial frequency, but opposite phase, as the corresponding fundamental component of the checkerboard. The reader may verify this himself by following the instructions given below the demonstration in *Fig.24*. Since the afterimage effect transfers interocularly, cortical, rather than retinal, mechanisms are probably involved. Interestingly, there seems to be no phase specificity in the interocular condition.

The checkerboard afterimage effect can be explained by the same mechanisms postulated above to explain the plaid pattern afterimage.

Let us assume that the adaptation to the checkerboard causes a phase specific response bias in the channels processing the diagonally oriented Fou-

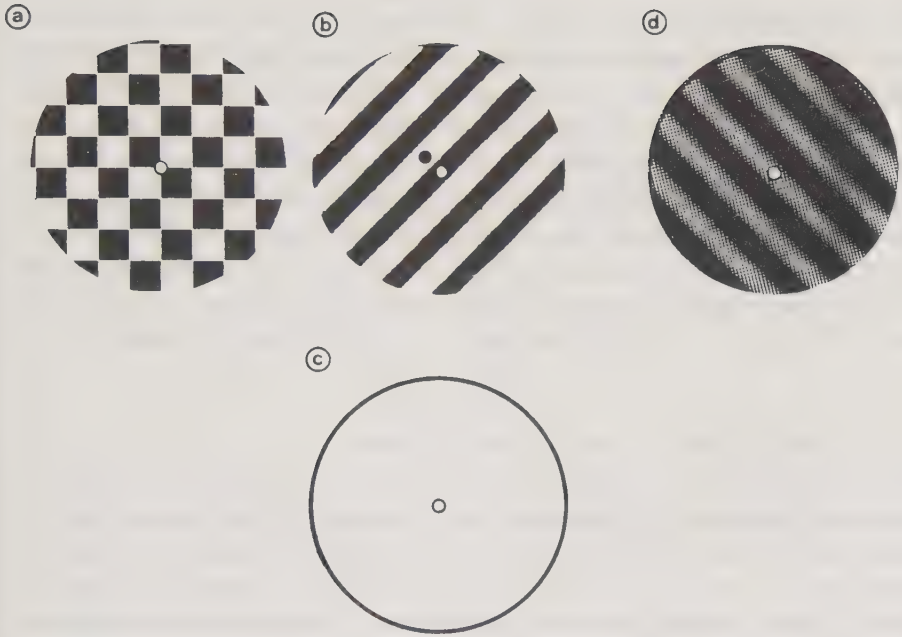


Fig. 24: Afterimages of the checkerboard fundamental Fourier components.

Fixate the point indicated in the center of the checkerboard (a) for about five seconds. Then shift the gaze to the white fixation point of the diagonally oriented grating (b), maintaining fixation for two seconds. Against a neutral background (c) there will appear a brief afterimage similar to the grating depicted in (d). The afterimage will be weaker if, instead of the white point in (b), the black one^e is fixated.

rier components. When a sine-wave grating, corresponding to one of these components, is subsequently presented, it will then inhibit the channels that were previously processing the other fundamental Fourier component oriented 90° to the sine-wave grating. When the sine-wave grating is then turned off, the release of inhibition in those channels will cause an 'disinhibitory enhancement' of the response bias. As a result, the fundamental Fourier component that is oriented 90° to the sine-wave grating will prevail

in the afterimage. That a stronger afterimage occurs for the counterphase sine-wave grating perfectly agrees with the notion that for counterphase conditions the inhibition, and consequently the disinhibitory response, is stronger too. It, therefore, seems reasonable to assume that the plaid pattern, as well as the checkerboard afterimage effect, are mediated by the same underlying mechanisms: that is, both effects can be best understood by postulating interactions between channels (neurones) tuned to the different orientations of the pattern Fourier components. This makes the primary visual cortex a good candidate for the locus of these effects, because it is the first stage at which neurones show a strong orientational selectivity.

4.2.5 More Evidence for the Cortical Hypothesis

There are two additional phenomena demonstrating that the diagonal Fourier components of the plaid pattern are processed by the visual system.

Under normal viewing conditions the diagonal Fourier components of the plaid pattern are not seen as separate elements. However, if one selectively modulates the luminance of the grey squares in the plaid pattern the diagonal components can be made visible: They appear to the observer just like the blurry diagonal grid of the afterimage superimposed on the grating. Such intensity modulation of the grey squares produces dramatic changes in the power of the diagonal Fourier components, which probably enhances their perception.

Another demonstration of the visual system's ability to process the diagonal Fourier components is given by a special moirée technique. If, after the adaptation to a static plaid pattern, a low contrast diagonal grid, with a spatial frequency slightly different from the plaid pattern's diagonal Fourier components is presented, the percept will be the following: Superimposed on the diagonal test grid will appear to be a grid of the same orientation, but with a lower spatial frequency. The repetition rate of this moirée grid will be identical to the spatial frequency difference between the plaid pattern diagonal Fourier components and the low contrast test grid. However, the moirée grid will only be present if a counterphase adaptation of the plaid pattern results in an diagonal afterimage grid. Further, the percept of the

moirée grid will remain the same, even if the subject is adapted to an image of the plaid pattern diagonal Fourier components (*Fig.1b*), instead of the pattern itself. Such a striking equivalence in results strongly indicates that the visual system is indeed processing the diagonal Fourier components of the plaid pattern. However, once again, it should be emphasized that only a length-integrating mechanism will be able to process these components. Neurones displaying such properties are first found in the primary visual cortex.

4.3 A Simple Model

A possible solution of how the visual system could process the diagonal Fourier components of the plaid pattern is given in *Fig.25a*. Three hierarchical stages are involved.

At the first stage, the light intensity falling onto sensors is transduced according to the quasi-logarithmic H-functions plotted in the insets.

The second stage integrates the output of the sensors, which are arrayed along a specific orientation (in this case 45°).

The third stage is a difference-operator which compares the output of two adjacent array integrators having the same orientation.

The input intensity distribution superimposed on the four sensors in *Fig.25a* corresponds to the plaid pattern. The connections between the sensor elements permit a representation of the pattern in terms of its diagonal Fourier components contrast at the difference-operator stage. As one can see, it is important that in the model the intensity values of the black and white squares, as well as those of the grey squares, are spatially integrated. If the intensity falling on all four sensors is the same (e.g. for a homogeneous field), the output of the difference-operator will be zero. This indicates that there is no contrast present. The output of the difference-operator will also be zero when the sum of transduced grey square's signals are equal to the sum of the signals coming from the black and white squares. But any increase or decrease in the grey squares intensity will cause the difference-operator to have an output, the sign of which will be determined by the direction of change.

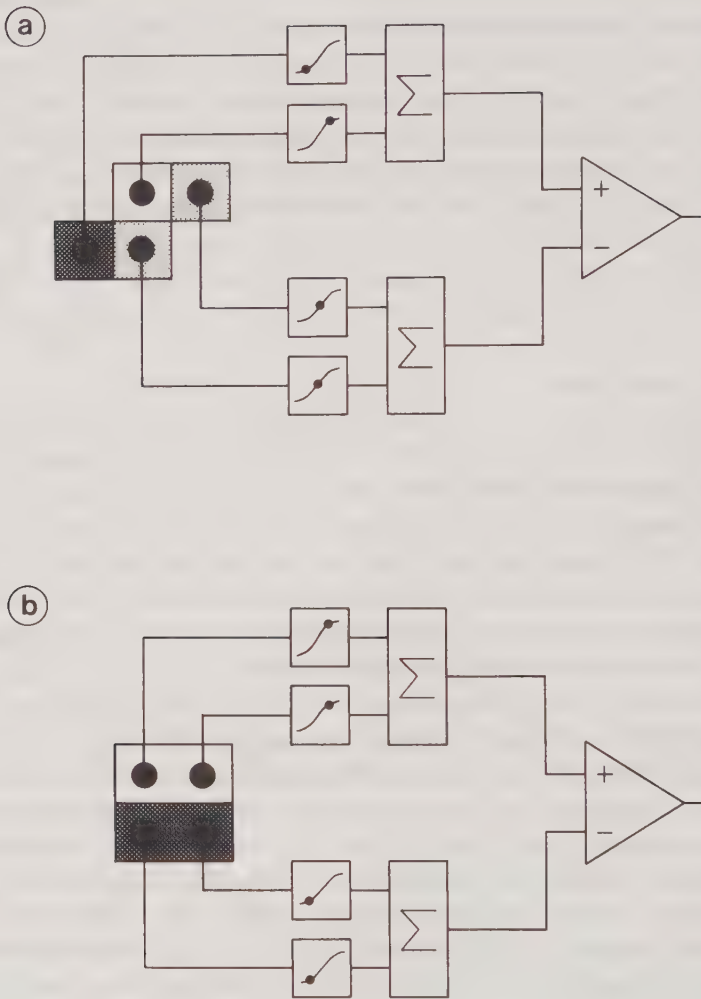


Fig. 25: A simple model.

- (a) processing of the plaid pattern's diagonal Fourier components
- (b) processing of a high contrast grating pattern.

In a system without intrinsic noise, even the slightest differences in the signals arriving at the difference-operator stage will be detected. On the other hand, in a system having intrinsic noise a difference in the signals will only be detected when it exceeds a certain limit (threshold).

Introducing intrinsic noise into the model is necessary if it is going to simulate the visual system's behavior in the plaid pattern experiment. With a fixed intensity of the black and white squares, there is a certain intensity range of the grey squares, for which the model will not signal the presence of contrast. The boundaries of this range will largely depend on the amount of intrinsic noise present in the system.

Let us now assume that the noise originates at the transducer stage and that it is constant for all signal levels. With a perfect logarithmic transducer function, which in log-linear coordinates can be represented by a function of constant slope, the error in intensity measurement will then be a constant fraction of the input amplitude. It can be shown that for these conditions the boundaries for detecting contrast at the difference-operator stage will remain the same at different contrasts of the black and white squares.

In the plaid pattern experiment, this means that the contrast thresholds for the diagonal Fourier components should be the same for all pattern contrasts. The results, however, are contrary to this prediction: They clearly demonstrate that the contrast thresholds increase with higher pattern contrasts. Can this observed increase be related to the particular shape of the transducer function? Although in a log-linear representation a H-function has an almost constant slope in its central region, the slope flattens considerably at its upper and lower ends. Consequently the error in processing intensity will be much higher in the outer regions, than in the central part of the function.

Given this high uncertainty in the signals coming from the black and white squares, the luminance located midway between them is defined less precisely. A plausible consequence of this is that the contrast thresholds for the diagonal Fourier components of the plaid pattern have to be higher when the differences between the black and white squares (i.e. for high pattern contrasts) are large.

A similar argument can be applied to ordinary contrast discrimination thresholds. An example is given in *Fig.25b*, where a grating, instead of a plaid pattern, provides the input. With increasing pattern contrast the black and white stripes will be processed more and more by the outer regions of the H-function (see inset plots). For higher base contrasts, an increase or decrease in contrast will produce smaller differences in output than for lower base contrasts. This is a consequence of the shallower slope of the H-function in its outer regions. The contrast discrimination thresholds are, therefore, also expected to increase with pattern contrast.

Thus, the striking similarity between conventional contrast discrimination thresholds and the contrast thresholds for the diagonal Fourier components measured in this study, can be both related to the specific shape of the H-function.

4.4 Why are Receptive Fields in the Visual Cortex elongated ?

The question 'why the visual system is designed the way it is' is of upmost importance to the understanding of biological systems, not only because it places the scientific data into a more general framework, but also because it provides a guideline for further research. The ultimate goal of the visual system, with all its transformations of the retinal intensity distribution, is to provide the organism with an unambiguous representation of the visual world. Presumably, given physical and biological constraints, nature has solved this problem in an optimal way.

At the retinal level the receptors transform the incoming light quanta into a graded electrical potential. Because the range of illuminations occurring in nature is enormous (they can vary by a factor of a billion), this represents a serious problem for the first transducer stage. The very elegant solution given by a dual receptor system and a variable range adjustment mechanism has been discussed in detail in the previous sections. An additional mechanism is the processing of physical light intensity in a quasi-logarithmic way (H-function). This serves to extend the response range of the receptors. However, a greater advantage seems to be that it allows the ratio of intensities (contrast) to be easily calculated as an additive integration of excitatory and inhibitory inputs.

The encoding of visual information in the contrast domain is advantageous because it is contrast and not absolute luminance which remains invariant under different levels of illumination. The ganglion cells, at the retinal output stage, already possess the property of contrast coding. In fact, the antagonistic organization of their concentric receptive fields entails a processing of light in terms of the ratio of intensities falling onto their centers and surrounds. This implies that a uniform background field, which equally stimulates the center and the surround, will be a poor stimulus for these cells. This is in fact the case.

(Since the receptive fields of the cells at the lateral geniculate nucleus (LGN) level are not very different from those of the retinal ganglion cells, a discussion of this stage will be omitted.

A major change in visual processing, however, occurs at the striate cortex, where the neurones are most efficiently stimulated by moving or flashing bars and edges of a specific orientation. Dots or disc stimuli, which are optimal stimuli at the retinal or geniculate level, elicit poorer responses. This preference of the cortical neurones is a consequence of their receptive field shapes, which are elongated rather than concentric (Hubel and Wiesel 1962, 1968).

The subdivision of striate cortical cells into those having distinct (simple cells) or less clearly (complex cells) defined excitatory and inhibitory regions, as well as other response features (hypercomplex cells), is not important to the present discussion. For clarity, therefore, further discussion will be restricted to the characteristics of simple cell receptive fields.

The once popular hypothesis that striate cortical neurones are feature detectors for edges and bars, no longer seems convincing because it (wrongly) implies the existence of detectors for curved and more complex contours. A more plausible hypothesis is that the cortical machinery transforms the retinal image into a code which resembles a local Fourier transform of a small patch in visual space. Supporting this hypothesis are the orientation, spatial frequency and phase (simple cells) specificities of striate cortical neurones. These properties can be regarded as a direct reflection of the receptive field shapes and profiles of these neurones: Orientation selectivity presumably results from the receptive fields' integration over length (elongated shape), frequency selectivity from their periodic weighting function in the width dimension (profile, antagonistic sidebands) and phase specificity from their fixed correspondence to the retinal mosaic.

If the visual system actually performs a local Fourier transform, what are the functional advantages of such a representation? Compared to a point by point representation of the visual image, for instance, a representation that integrates over length will presumably cause a loss of positional information. For example, since a small spot of light will elicit a similar response anywhere along the excitatory band of a simple cell's receptive field, the spot's exact position within the cells receptive field will be lost. However, such local information can be regained by taking into account the responses of other neurones, whose receptive fields occupy the same location, but integrate along different orientations. Thus the information about a point

in visual space will be distributed across a whole population of neurones and the point's specific position will not be lost.

There is a striking similarity between this procedure and Computerized Tomography, in which a local density value is also reconstructed from the integrated absorption curves over different orientations. Of course, in the visual system not local density values, but the distribution of intensity values has to be represented. Thus, the analogy, although compelling, does not actually explain why the visual system should use such a strategy. In contrast to Computerized Tomography, the visual system can directly access local information. Integration itself, however, offers an advantage, which should not be underestimated.

The retinal 'screen' is far from perfect. Before light reaches the receptors, it has to pass through the whole retinal network, including the vascular system. These obstructions will cause the image at the receptor mosaic level to be greatly deteriorated. A point by point analysis of the retinal image, therefore, would result in these obstructions being directly encoded in the visual image. On the other hand, an analysis utilizing spatial integration will not only reduce these unwanted impediments (by averaging), but will also provide a means of eliminating small imperfections. In the following discussion it will be demonstrated that the way in which this can be accomplished is quite simple.

Let us assume that simple cells integrate linearly across their receptive fields (evidence for this is given by several investigations, see De Valois, Albrecht and Thorell, 1978; Movshon et al., 1978; Kulikowski and Bishop, 1981; Schumer and Movshon, 1984).

If a simple cell, with a receptive field like the one depicted in *Fig.26*, is stimulated with a bright bar which exactly fills its excitatory band (*Fig.26a*), it will respond maximally. Because of the cell's integration properties, a reduction of the bar's length will proportionally reduce the cells response (*Fig.26b*). The response to a 'full size' bar will also be reduced, if, for example, a blood vessel runs through the cell's receptive field (*Fig.26c*). In order to represent the stimulus adequately in this case, all the cell has to do is to adjust its gain, so that a maximal response is reestablished. Such a mechanism would be equivalent to interpolating across the small scotoma produced by the blood vessel.

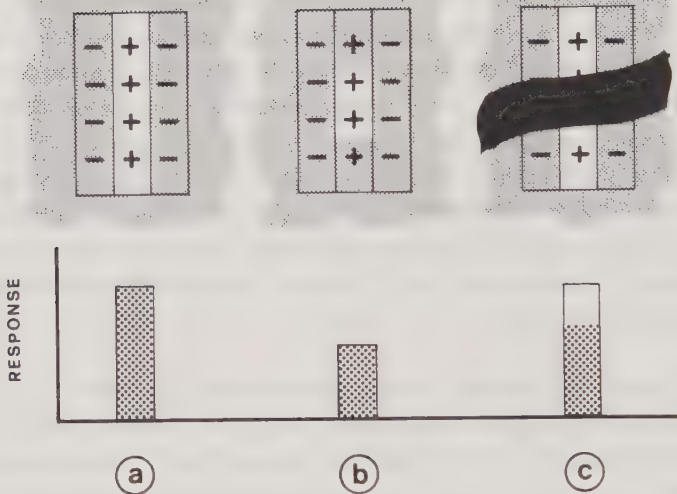


Fig. 26: Interpolation across a receptive field's length dimension

Nevertheless, there are two major problems with postulating such a mechanism. The first problem is that in principle the visual system cannot distinguish between a blood vessel and a visually relevant stimulus. The second is that the gain adjustment mechanism (and consequently interpolation) will break down if the blood vessel runs directly through the excitatory band. The first problem would be eliminated if there existed an easy way to distinguish visually relevant stimuli from blood vessels and other obstructions. In that case, the visual system would just have to ignore structures whose relative retinal location is fixed. The fast fading of stabilized images (e.g. Koenderink, 1972), but also of afterimages, supports the existence of such a mechanism in the visual system.

The second problem would be eliminated if, in addition to length integration, there existed integration across the width domain of a receptive field. A possible substrate for such a mechanism could be the spatial weighting function, resulting from the the excitatory and inhibitory bands in simple

cell receptive fields. Indeed, there is some evidence that the receptive field profile of simple cells not only consists of a single center-surround organization, as shown in *Fig.26*, but also of additional, antagonistically organized, side-bands (De Valois et al., 1978; Movshon et al. 1978; Andrews and Pollen, 1979; De Valois et al., 1985). (The further physiological distinction of receptive fields into odd (e.g. an excitatory and an inhibitory region of similar valence) and even symmetrical field profiles (a center region with symmetrically organized antagonistic surrounds) has no importance for the present argument and will therefore be neglected.)

The presently popular notion is that the profile of these multiple side-band receptive fields can be best described by a Gabor-function, which is a sine or cosine weighted with a Gaussian (e.g. Daugman, 1985). An example of such a function (cosine phase) is given in *Fig.27*. In a cell with such a receptive field profile integration in the width domain results from the fact that the different excitatory and inhibitory zones sum up to a single response. A stimulus giving a maximal response will be a grating whose repetition rate (spatial frequency) of bright and dark regions exactly matches the one of the receptive field profile.

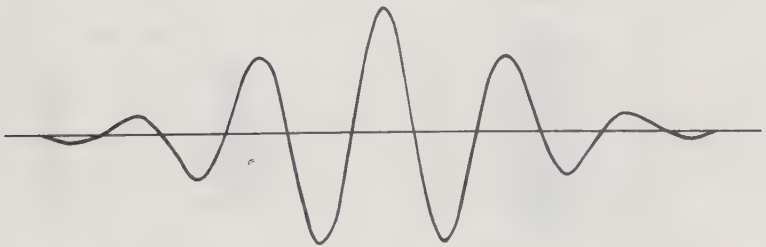


Fig. 27: The Gabor function

This is demonstrated on the left side of *Fig.28a*, where a square-wave grating is superimposed on a receptive field in an optimal way. On the right

side of *Fig. 28a*, the corresponding receptive field profile and the luminance profile of the square-wave function (dotted lines), as well as the response of the hypothetical cell, are shown. If a blood vessel covering the center excitatory band of the receptive field, is introduced, the overall response of the cell will be diminished (*Fig. 28b*). In order to regain the original response to the grating, the cell can adjust its gain by increasing the valence of its side-bands (*Fig. 28c*). Thus the cell will respond as if there was no obstacle. This mechanism is equivalent to interpolating across the receptive field's width in the spatial frequency domain.

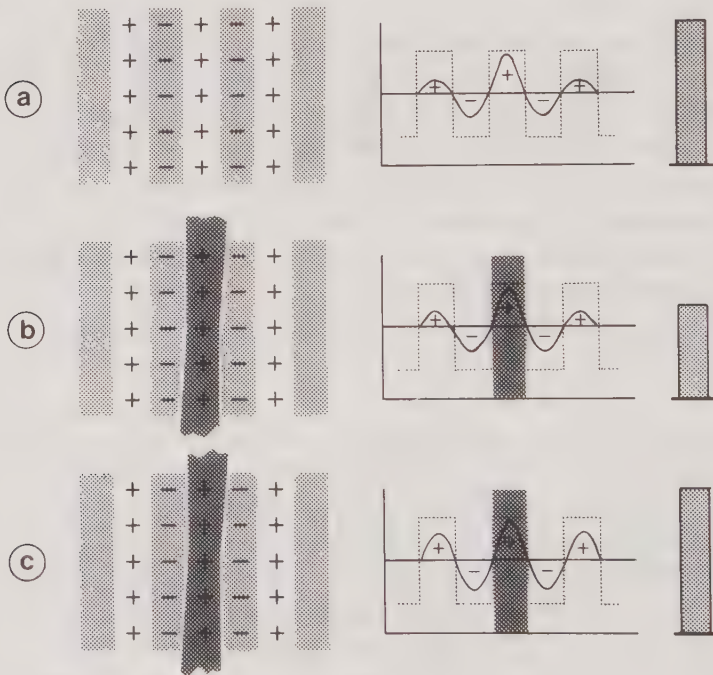


Fig. 28: Interpolation across a receptive field's width dimension

Taken together, the integrative properties of simple cells along the length and width dimensions provide a basis for interpolatory processes, which possibly prevent small obstructions, regardless of their shape or orientation, from being perceived. There are, of course, many if's and but's aris-

ing from the simple and certainly incomplete examples given above. However, the intention was not so much to provide an elaborate model as to sketch out a possible explanation.

The many completion phenomena observed in clinical diseases such as retinosis pigmentosa or during migraine attacks (Kuffler and Nicholls, 1976), suggest the presence of interpolatory processes in the visual system.

It seems reasonable to also relate the afterimage effects of the present investigation to such mechanisms. Since the phase of the plaid pattern's diagonal Fourier components remains constant during adaptation, the system could assume that these components are not part of the image, but rather signals to be cancelled out. The response bias introduced by these components would then be a reflection of a retuning process (gain adjustment) and not of an intrinsic, unwanted 'memory' property of the system. Since the phase locked signals are not located in the retina itself, the viewing of a neutral background would cause the appearance of an 'afterimage' of these retuning processes.

It should be seen from above that the properties of striate cortical neurones are compatible with a representation of the visual image in terms of a local Fourier spectrum. It seems unlikely that the advantages of such a transform are solely the interpolatory processes discussed above. For one thing, orientationally-selective filters themselves provide an advantage by reducing the noise in the image (Torre and Poggio, 1985). For another, the redundancies in natural images can be best dealt with filters which match these properties. In this regard, Bossomaier and Snyder (1986) have recently argued that a local Fourier transform in terms of two-dimensional Gabor patches (similar to simple cell receptive fields) is an appropriate way to deal with the statistical redundancy in images. For example, since many contours in a natural surround are line or straight-edge segments, a sampling in terms of orientationally-selective filters will reduce the analysis of an edge and its orientation to a single step.

A further argument in favor of a Fourier-like analysis is that the information for a specific point in visual space is distributed over a whole population of neurones (filters). Thus a failure of only a few neurones in the visual cortex will not cause an entire loss of information about the point in space, as would be the case for a point by point representation.

It still is unclear what advantages a local Fourier transform of the image would have for the processing stages beyond the primary visual cortex. A clarification of this issue is certainly one of the most interesting and challenging tasks for further research.

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SUMMARY

An ordinary plaid pattern is equivalent to the linear superposition of vertical and horizontal square-wave gratings. It consists of black, white and grey squares, with the luminance of the grey squares being identical to the arithmetic mean of the luminances of the black and white squares. Counter-phase adaptation to such a pattern generates a diagonally oriented afterimage grid, which closely resembles the fundamental Fourier components of a checkerboard. The presence of the diagonal afterimage grid is surprising because the Fourier spectrum of the ordinary plaid pattern contains only the vertical and horizontal components of the composite square-wave gratings; and not the diagonal fundamental components of a checkerboard. The diagonal afterimage grid, however, can be explained by assuming a non-linear transduction of luminance in the visual system, which would introduce a distortion into the luminance relationships between the plaid pattern elements. In the Fourier domain, such a distortion is equivalent to introducing a checkerboard spectrum. If such a distortion exists, then it should be possible to eliminate the checkerboard spectrum, and hence the diagonal afterimage grid, by setting the luminance of the grey squares to a value that corresponds to the mean of the transduced luminances of the black and white squares.

This was tested by finding the luminance range for the grey squares that produced no diagonal afterimage grid following adaptation to the plaid pattern. Measurements were made in 3 subjects for 80 plaid patterns, differing in contrast from 0.1 to 0.8 and in pattern-average luminance from 0.022 to 22.0 cd/m². The mean relative luminances of the grey squares producing no afterimage were used to infer the luminance transducer properties, while the luminance ranges in which no afterimage occurred were used to calculate the contrast thresholds for the checkerboard fundamental components.

In the main experiment, white-light patterns were used to generate the wide range of pattern-average luminances and pattern contrasts. Under all conditions the relative luminance of the grey squares producing no afterimage was very close to the geometric mean of the black and white squares. Such a relationship suggests a quasi-logarithmic processing of luminance. However, very small deviations from a logarithmic function were found. In general these deviations varied systematically with pattern-average luminance and pattern contrast. The largest deviations (around 10%) were found for high contrast plaid patterns at the moderate and high pattern-average luminances tested. At the low pattern-average luminances tested, the deviations showed a discontinuity which was present for all pattern contrast conditions.

The hypothesis that the discontinuity is related to the transition from cone- to predominantly rod-mediated vision was confirmed in a second experiment: Long-wavelength (red) plaid patterns were used to isolate the cone system; thus permitting the cone transducer characteristic to be revealed at lower pattern-average luminances, unobscured by the rod system. The results of the red-light experiments clearly demonstrate that the cone system reaches its sensitivity limits near the point where the discontinuity occurs in the white-light experiments. Furthermore the red-light data provided a basis for determining the exact shape of the cone transducer function at its lower end.

It was concluded: (i) that the cone transducer function (and possibly also the rod transducer function) is best modelled by a sigmoid (i.e. a H-function) with a dynamic range of approximately ± 1.5 log units and (ii) that the cone transducer function, in order to maintain maximum sensitivity, shifts along the intensity axis with increasing ambient illumination. Such a range-adjustable function has already been proposed to explain the response properties of retinal receptors.

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